学位申請論文

Ecological studies on Japanese Hosta
(日本産ギボウシ属植物の生態学的研究)

藤田 昇

主論文 1

HABITAT AND WATER ECONOMY OF JAPANESE HOSTA

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Synopsis

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To study the ecological adaptation of the Japanese Hosta, the habitat preference and water economic characteristics of a number of species are determined and compared. Stomatal density and size, transpiration rate, drought resistance and relative growth rate in seedlings are investigated as indicators of adaptation to the soil moisture conditions of the habitat. The species which commonly occur under a diversity of soil moisture conditions, for example, H. sieboldiana, can readily adapt their water economies to a wide variety of environments, showing fairly high transpiration rates, rather high drought resistance and high relative growth rates. They can be regarded as ecologically unspecialized. On the other hand, with the exception of H. capitata, the species restricted to relatively dry habitats such as stony outcrops and rocky soils, for example, H. kikutii and H. longipes, have low transpiration rates and low relative growth rates in spite of high drought resistance. Finally, H. longissima, which is confined to wet places, exhibits low drought resistance, with a high transpiration rate and a somewhat high relative growth rate. The species which grow in limited habitats have rigid water economies, though each is well adapted to its particular environment. Thus, they may be considered ecologically specialized.

Introduction

The genus Hosta(Liliaceae), consisting of perennial herbs, is endemic in East Asia. It is particularly differentiated in Japan, where 15 species have been identified(Fujita, 1976). Japanese species of Hosta are found at forest margins and in canopy openings, grasslands, moors, valleys and so on. The character of the substratum is also a factor in determining whether the species live epiphytically on rocks or terrestrially on soils. Thus their habitats are diverse, particularly soil moisture conditions, which range from extremely wet to relatively dry.

Present-day species have arisen through the course of evolution with the change of life, and they are well adapted to their environments(Darwin, 1859). In studying the life of any species, it is first necessary to analyze the habitat of the species and to determine how it has adapted itself to its environment. In addition, since the evolution of species is restricted by phylogeny and many aspects of the life of each species can be understood by comparison with closely related species, a comparison of the ecology of species bearing close systematic relationships, such as those belonging to a genus, is a significant and effective approach. In Hosta, therefore, a partial understanding of the life of each species can be obtained by investigating the extent to which its habitat ranges, how it adapts itself physiologically to soil moisture conditions and comparing this data with that obtained with closely related species.

In this paper the habitat range and the water economy of each species are determined and used as a basis for their relationships among the species examined from the viewpoint of adaptation.

Habitat

All the species of japanese Hosta were compared for habitat

preference. To what extent each species may occur in different types of habitat may be judged from data collected over the whole range of distribution in Japan, which is listed in Table 1. Each species has its particular preference for habitat, and differences in habitat range are found among the species. Generally, the species may be classified into three types, mainly on the basis of prefered soil moisture conditions: (1) those living under a diversity of soil moisture conditions, (2) those restricted to wet places, and (3) those confined to relatively dry places, such as outcrops and rocky soils. There is also a good correlation between habitat range and abundance of Hosta species. The species of the first type, which have broad habitat ranges are more abundant than those of the other two types. H. sieboldeana is representative of the first type. H. albomarginata, and H. kiyosumiensis and H. tsushimensis rank next to it in versatility, though the first has a tendency to grow in moist places, while the other two grow infrequently in wet places. H. longissima and H. alismifolia are included in the second type. The other species all belong to the third type, with minor differences among them.

Table 1

Water Economy

Materials and methods

To study water economy, stomatal density and size, transpiration rate, drought resistance and growth rate were measured. Except for the stomatal characteristics, comparisons of water economy among the species were made by using seedlings to exclude age differences. H. alismifolia and H. tardiva which are sterile, and H. pulchella, seeds of which were unavailable, were not examined. Both adult plants and seedlings were used for stomatal measurements.

Stomatal density and size, and the stomatal index, or the ratio

of epidermal cells to stomata, were determined with leaves collected from native sites throughout the range of distribution. The center of a half blade of the most fully expanded leaf of a plant was measured by the stamping method. Most Hosta species have stomata only on the lower surface of the leaf, but some species, which grow in wet habitats and hold their leaves more erect, possess stomata on both surfaces. In these species, stomatal density was calculated from the total of both sides. Stomatal index was derived from only the lower surface.

Seedlings of 12 species were grown from seeds gathered from native sites and planted in sandy loam soil in pots in a greenhouse where the air temperature ranged from 15 to 27°C. The soil moisture during growth was maintained at one of the following three levels: (1) high level, 95-85%; (2) median level, 65-55%; and (3) low level, 35-25% based on the maximum water capacity which was 44% on dry weight base after 5 days' drying at 105°C.

After dehydration to various degrees by withholding soil moisture, seedlings about 60 days old which had three mature leaves were used for transpiration measurement by the pot-weighing technique. After covering the soil surface of the pot containing a seedling with rubber cloth, evapo-transpiration was estimated from the change in weight of the pot during 12 hr in a growth room under conditions such that the light intensity on the seedling top was 20 klux, the air temperature was 26°C and the air saturation deficit was ca. 13 mm Hg. To determine evaporation from the soil surface through the small opening between the petioles of the seedling and the cover, the weight change of a pot treated similarly except that a plastic pole was put in the soil in place of a seedling was measured. Transpiration was evaluated as the difference between evapo-transpiration

and evaporation. Just after the experiment, the fresh weight of the leaves and their leaf area were measured. Then the third leaf of the seedling was measured for stomatal density and size by the same method applied to adult leaves, and the dry weight of the leaves was obtained after 3 days' drying at 95°C. Transpiration rates were expressed in terms of leaf area, because leaf area is said to be the best basis for expressing transpiration rates when comparisons are made between plants of different species(Kramer, 1969).

Drought resistance was judged from the survival time of the detached leaf and that of the whole seedling under drought conditions. The third leaf was cut off from the seedling raised under the median level soil moisture, and the cut end of the petiole was sealed immediately with vaseline. Then the leaf was exposed to the air in the growth room with a photoperiod of 12 hr. The other experimental conditions were the same as given in the transpiration experiment. The leaf was weighed at the start of the experiment and reweighed every day. Since there was little change in the dry weight of a leaf during an experiment, water contents of the leaf during the experiment were determined on the basis of the fresh weight of the living leaf in the course of the experiment and the dry weight of the dead leaf at the end of the experiment. The lethal water content of the leaf in each species was found from that of another leaf treated alike, whose death was judged from TTC(2, 3, 5-triphenyltetrazoliumchloride) stainig. Survival time of the whole seedling was measured in the greenhouse, using potted seedlings of the same age as employed in the transpiration experiment. After stopping water supply to the soil in pots, seven seedlings at a time were harvested at 2 days' intervals till the death of seedlings in each species, and the water content of leaves was determined. Lethal water

content of the leaf in the whole seedling was obtained from another seedling as in the case of the detached leaf.

In parallel with these experiments, seedlings of each species were cultivated in pots in the greenhouse for growth experiments under the following two conditions of soil moisture: (1) 80-50% on the basis of the maximum water capacity, keeping the soil continuously moist; and (2) 80-20%, making the soil drier. In both cases the soil was supplied with water up to the maximum moisture when the soil moistures decreased to the respective minimums. For the measurement of biomass, seedlings were gathered 60 days after planting of seeds, when the third leaves had fully developed. Seedling growth was determined from the relative growth rate shown as the ratio of seedling biomass to that of one seed.

Results

Stomata.

As for the stomatal structure, there was little difference among the species. Stomatal density and size of the adult leaf are given in Figs. 1, 2 and 3. It was observed that although stomatal density and size are fairly variable within each species, the values fell into clusters which were distinctive for each species. In addition, it is evident that there are species differences related to habitat differences. Among the species living in relatively dry habitats, *H. longipes*, *H. capitata* and *H. pulchella* exhibit quite large but few stomata, while *H. kikutii*, *H. tardiva* and *H. shikokiana* have many small stomata, and *H. hypoleuca*; *H. tibai* and *H. pycnophylla* show small but few stomata. On the other hand, large and very frequent stomata are seen in *H. albomarginata*, *H. longissima* and *H. alismifolia*, which inhabit wet places. *H. sieboldiana*, *H. tsushimensis* and *H. kiyosumiensis* display large and fairly frequent

Fig. 1
Fig. 2
Fig. 3

stomata. The same pattern was observed in the case of seedling stomata, as indicated in Fig. 4. Fig. 4

Stomatal index is presented in Table 2. The stomatal index showed less variation in each species than the stomatal density and size, and little differnce among the species relevant to habitat difference was observed. Table 2

2. Transpiration rate.

Figs. 5 and 6 show transpiration rates in relation to the water contents of seedling leaves under the median level soil moisture. Fig. 5 Fig. 6 It is seen that a reduction in the water content of the leaf caused by a decrease in the soil moisture reduced the transpiration rate in every species examined, but species differences are found in the following three respects: (1) transpiration rate under sufficient water supply, (2) reduction rate of transpiration with decreasing water content of the leaf, and (3) percentage of water content of the leaf under moist soil conditions. According to these features, the 12 species may be generally grouped into the following five types:

(1) H. pycnophylla, H. hypoleuca and H. tibai, which show very low transpiation rates, high reduction rates and high leaf water contents;

(2) H. kikutii, H. longipes and H. shikokiana, which have low transpiration rates, high reduction rates and low leaf water contents;

(3) H. sieboldiana, H. kiyosumiensis and H. tsushimensis, which bear fairly high transpiration rates, high reduction rates and rather high leaf water contents;

(4) H. albomarginata and H. longissima, which exhibit high transpiration rates, low reduction rates and low leaf water contents; and

(5) H. capitata, which display a low transpiration rate, a low reduction rate and a low leaf water content.

To determine whether the soil moisture level during the growth of the seedlings had affected the above features, relations between

transpiration rate and leaf water content were compared among seedlings grown under the three different conditions of soil moisture mentioned above. Fig. 7 shows the results with H. longissima and H. longipes, which were chosen as typical species whose habitats were confined to wet and relatively dry places, respectively. It appeared that the relations varied in each species according to the soil moisture during growth, but that the defference between these two species was constant regardless of the moisture content of the soil. Moreover, to check the intraspecific variation of this relation attributable to any habitat differences, e.g. soil moisture, the relation was compared among H. sieboldiana seedlings from different habitats, since this species has the most varied habitats. Fig. 8 shows that the observed variation is small. Therefore, it may be safely said that the characteristics of each species indicated in Figs. 1 and 2 are peculiar to it to a large extent.

Fig. 7

Fig. 8

3. Drought resistance.

The reduction in the water contents of excised seedling leaves is given in Fig. 9, and that of potted seedling leaves is shown in Fig. 10. As for the lethal water content of the leaves, no significant species variation was found in either type of leaves, though it was lower in the excised leaves than in the potted seedlings, probably because of slower water loss in the latter. In contrast, species differences were clearly seen in the survival time, which showed the same tendency in both types of leaves. Long survival time was seen among the species growing in relatively dry habitats, with the exception of H. capitata, [H. kikutii, H. pycnophylla, H. hypoleuca and H. tibai exhibited particularly long survival. On the other hand, a short survival time was shown by H. capitata and the species inhabiting wet places. Long survival is ascribed

Fig. 9

to slow water loss during the drought and the high water content of leaf before drought. The degree of drought resistance may be gauged by the length of survival time.

4. Seedling growth.

Seedling growth of each species under moist and dry soil conditions are listed in Table 3. High relative growth rates under the moist soil condition were shown by the species living in varied habitats and exhibiting high transpiration rates. Consequently there appears to be a parallel between the relative growth rate and the transpiration rate. A reduction of the relative growth rate under dry soil conditions relative to that under moist soil conditions was seen in all the species, though the rate of decrease was lower in the drought-resistant species.

Table 3

5. Grouping of the species.

Twelve species of Hosta may be classified roughly into four groups on the bases of water economic characteristics and habitat range, as shown in Table 4. The species having wide habitat range, or occurring in varied habitats, display a fair measure of ability in every water economic characteristic, whereas those limited in habitat range are defective in some aspect of their water economy. H. longissima, which is restricted to wet habitats, is highly susceptible to drought, exhibiting a high transpiration rate and a somewhat high relative growth rate. Except for H. capitata, the species confined to outcrops and rocky soils have low transpiration rates and low relative growth rates, and are very resistant to drought. H. capitata is inferior to all the others in all the water economic abilities, in spite of living in rocky places.

Table 4

Discussion

It is considered difficult to generalize about the significance of stomatal density and size in connection with water relations. It is said that smaller and more frequent stomata are characteristic of xeromorphism(Shield, 1950). According to Monshi(1944), there is no close relationship between stomatal density and size, and drought resistance of plants, though plants are different from one other in stomatal characteristics. Salisbury(1927) proposed to use the stomatal index as a parameter independent of environmental factors because stomatal characters vary within plants depending on environmental conditions(Eckerson, 1908; Gupta, 1961; Knecht & O'leary, 1972). He maintained that helophytes were characterized by a low stomatal index, and xerophytes by a high one. As far as Hosta is concerned, the results show that stomatal density and size correlated well with the transpiration rate of the species when abundant water is supplied, and that a general correlation with other water economic characteristics is not found. Frequent and large stomata are seen in the species which have high transpiration rates, such as H. longissima, while few or small stomata are observed in the species which, like H. longipes or H. kikutii, display low transpiration rates; and further, very low transpiration rates are shown by the species bearing few and small stomata, for example, H. hypoleuca. As for stomatal index, no species difference relevant to any differences in habitat preference and water economic characteristics is found, although the stomatal index may show less variation within species than stomatal density and size.

It was reported that, under moist soil conditions, drought-resistant plants did not necessarily transpire less than plants of the mesophyte type grown under the same conditions, and that

transpiration rate is not suitable for judging drought resistance of plants(Maximov, 1929; Miller, 1938; Turrel, 1944; Tazaki, 1960). In the case of Hosta, many drought-resistant species, especially all the species most resistant to drought, i.e., H. kikutii, H. pycnophylla, H hypoleuca and H. tibai, certainly exhibit low transpiration rates even when supplied sufficient water. However, H. sieboldiana, H. kiyosumiensis and H. tsushimensis, which grow in varied habitats, have fairly high transpiration rates in spite of rather high drought resistance. H. capitata shows low drought resistance, although it transpires slowly. Therefore, in Hosta, drought resistance usually does not correlate with transpiration rate under moist soil conditions.

It is well known that reducing water loss during drought is one of the ways of postponing plant water stress(Kozlowski, 1964; Kramer, 1969; Larcher, 1973). The results show that the drought resistance in Hosta may be attributed mainly to slow dehydration under drought conditions, as seen with other plants(Boon-Long, 1941; Parker, 1951; Iljin, 1953; Jarvis & Jarvis, 1963).

A clear account has not been given of the relation between transpiration rate and growth rate, though a positive relation was suggested by Winneberger(1958). It is apparent from the growth experiments that high relative growth rates are seen in the species which transpire rapidly under moist soil conditions, but the converse does not necessarily hold true; for H. longissima has a relative growth rate that is only slightly elevated notwithstanding vigorous transpiration. This suggests that rapid transpiration is necessary but not sufficient for fast growth. In addition, Grime & Hunt(1975) reported that high relative growth rates of seedlings are involved in competitive and ruderal strategies in plants, whereas low ones characterize the

strategy of stress-tolerant plants. It is noteworthy, in this connection, that the Hosta species growing in varied habitats have high relative growth rates, while, in contrast, the species which occur in limited habitats show low ones.

In Hosta, the species which commonly grow under various habitats soil moisture conditions are readily adapted to different natural soil moisture conditions, showing not only rather high drought resistance but also fairly high transpiration rates and high relative growth rates. On the other hand, the species occurring in restricted habitats are deficient in water economic flexibility, though, except for H. capitata, they adapt themselves rigidly to a particular environment. Tabata(1964) emphasized the specialization-generalization aspect of evolutionary changes with reference to the life of species. From this ecological viewpoint, the Hosta species with broad adaptability may be regarded as unspecialized or generalized, and the ones with only a narrow adaptability range as specialized. H. capitata, which displays low drought resistance as well as a low transpiration rate and a low relative growth rate, is not well adapted to any type of environment in its water economic abilities.

As Parker(1968) pointed out, many species of plants, all growing in one habitat, have so many different adaptations which interblended with each other that it is practically impossible to define them as one term. Hence, it follows that it is still more difficult to draw comparisons of water economy among species growing in different habitats. However, this difficulty may be minimized if, instead of species from different phyletic lines, species closely related morphologically and physiologically are chosen for analysis. With such systematically related groups of species as the Japanese Hosta species, the ecological significance of water economic characteristics in each species may be effectively

deduced from a comparative analysis of water economy in relation to habitat.

Summary

1. The species of Japanese Hosta are found to differ from one other in habitat range, particularly with respect to preferred soil moisture conditions. There is a positive correlation between habitat range and abundance of the species.

2. Seedlings of 12 species are used for determination of water economic characteristics, namely, stomatal density and size, transpiration rates under different soil moisture conditions measured by the pot-weighing technique, drought resistance judged from the length of survival time under drought, and relative growth rates under moist and dry soil conditions.

3. The species are compared for relationships between habitat preference and water economic characteristics from the viewpoint of adaptation, and in connection with this, the ecological specialization of each species is considered.

4. Briefly emphasized is the effectiveness of comparative studies of related species in the understanding of the life of species.

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摘　要

1、日本産ギボウシ属植物各種の生育場所を調査し、生育場所の環境条件として、主として土壌水分条件に関して種間に違いが見られた。その中で、乾生から湿生まで生育場所の幅が広く多様な種が、最も普通に見かけられるものである。

2、生育場所の土壌水分条件への対応として、各種の水分経済特性を調べた。気孔の密度と大きさ、様々な土壌水分条件下での蒸散速度、乾燥条件下での生存時間から判断した耐乾性、適湿及び乾燥土壌条件下での相対成長率に関して芽生えを用いて測定した。

3、オオバギボウシなど生育場所が多様な種は、蒸散速度と耐乾性がかなりたきく、相対成長率は最もたきく、水分経済適応性の幅が広く生態的に特殊化していないといえる。一方、ミズギボウシのように湿地に限られる種は、蒸散速度はたきく相対成長率も少し大きいが、耐乾性は小さかった。また、ヒュウ

ガギボウシなど岩上のように比較的乾燥ところに限られる種は、蒸散速度と相対成長率は小さく、耐乾性は大きかったが、カンザシギボウシのみは、耐乾性も小さかった。このような種は、程度の差はあっても、生態的に特殊化しているといえる。

4、種の生活を捉えるうえで、近縁種間で比較することの有効性を指摘した。

Fig. 1. Stomatal density and size of adult leaves of Hosta. Each point shows the mean value of 5-10 plants in a population. Populations are selected to cover the whole range of distribution and habitat of each species.

Fig. 2. Stomatal density and size of adult leaves of Hosta. Notes as Fig. 1.

Fig. 3. Stomatal density and size of adult leaves of Hosta. Notes as Fig. 1.

Fig. 4. Stomatal density and size of the third leaf of seedlings used in transpiration experiments. Each point represents one individual.

Fig. 5. Relationships between transpiration rates and water contents of leaves examined under different soil moisture conditions. Each point stands for one experiment. Localities are as follows: H. longissima, Kakogawa(Hyogo Pref.); H. longipes, Kitakomatsu(Shiga Pref.); H. sieboldiana, Mikata(Fukui Pref.); H. pycnophylla, Ooshima (Yamaguchi Pref.).

Fig. 6. Relationships between transpiration rates and water contents of leaves tested in the same way as in Fig. 5. Each curve represents the avarage of 12-20 experiments in each species. Localities are given as under: H. tsushimensis, Izuhara(Nagasaki Pref.); H. capitata, Miyodo(Kochi Pref.); H. kikutii, Yanase(Kochi Pref.); H. hypoleuca, Horai(Aichi Pref.); H. albomarginata, Unomachi(Ehime Pref.); H. shikokiana, Akaishi(Ehime Pref.); H. kiyosumiensis, Ise (Mie Pref.); H. tibai, Inasa(Nagasaki Pref.).

Fig. 7. Effects of three soil moisture conditons during growth on the relationships between transpiration rates and water contents of leaves. Localities are as in Fig. 1. The soil moisture conditions are as follows: wet, 95-85% on the basis of the maximum water

capacity; median, 65-55%; dry, 35-25%.

Fig. 8. Intraspecific variation of relationships between transpiration rates and water contents of leaves attributable to havitat differences as to the soil moisture condition. Localities and habitats are as follows: Mikata(Fukui Pref.), fairly wet places in a stream bed; Hirasan(Shiga Pref.), rather dry, rocky soil on mountain ridge; Chomonkyo(Yamaguchi Pref.), dry rock cliff in a valley; Tenshigadake(Shizuoka Pref.), moist grassland on a mountain slope.

Fig. 9. Changes of water content of the excised leaf after detaching. Each point shows the mean value of five leaves. The lethal water contents of the leaf are found between the two isopleths A and B.

Fig. 10. Changes of water content of the potted seedling leaf under drought derived from stopping the water supply to the soil in pots. Each point represents the average value of seven plants. The lethal water contents of the seedling leaf are given between the two isopleths A and B.

Table 1. Occurrence of each species on different habitat types according to data gathered from the whole range of distribution in Japan. The frequency of occurrence is given as follows: H, 30 percent or more of the total occurrence of each species; L, less than 30 percent; blank, hardly any or none.

Species	Habitat type						
	Moor	Grass-land	Forest margin and canopy opening	Valley	Rock	Rocky soil	Soil
H. sieboldiana (Lodd.) Engler	L	H	H	H	H	H	H
H. kiyosumiensis F. Maekawa		L	H	H	H	H	H
H. kikutii F. Maekawa				H	H	L	
H. pycnophylla F. Maekawa		L	H		L	H	
H. hypoleuca Murata				H	H		
H. longipes (Franch. et Savat.) Matsumura		L	H	H	H		
H. albomarginata (Hook.) Ohwi	H	H	H	L	L	L	H
H. longissima Honda ex F. Maekawa	H						H
H. alismifolia F. Maekawa	H						H
H. pulchella N. Fujita			H		H	L	
H. tsushimensis N. Fujita		L	H	H	H	H	L
H. tibai F. Maekawa			H	L	H	H	
H. tardiva Nakai		H	H		H	H	
H. shikokiana N. Fujita		L	H		H		
H. capitata (Koidz.) Nakai			H	H	H	L	

Table 2. Stomatal index of adult leaves of *Hosta*. Each figure stands for the mean value of three plants in a population with its standard deviation. The number of populations are given in parenthesis. The populations are selected to cover the whole range of distribution and habitat of each species.

Species	Stomatal index
H. sieboldiana	15.4±2.6 (24)
H. kiyosumiensis	15.7±2.6 (24)
H. kikutii	16.9±1.4 (20)
H. pycnophylla	16.6±2.0 (3)
H. hypoleuca	18.6±1.6 (3)
H. longipes	13.0±1.5 (15)
H. albomarginata	16.3±2.0 (25)
H. longissima	17.3±1.6 (8)
H. alismifolia	17.0±1.0 (2)
H. pulchella	13.8±1.1 (2)
H. tsushimensis	15.3±1.8 (6)
H. tibai	14.2±0.8 (3)
H. tardiva	14.7±1.2 (10)
H. shikokiana	20.8±2.0 (6)
H. capitata	12.6±1.6 (6)

Table 3. Seedling growth under moist and dry soil conditions. Seedling biomass was measured 60 days after planting of seeds. The biomass of seed and seedling is expressed as mg DW/seed or seedling. Each figure shows the mean value of 100 seeds or 20 seedlings. Relative growth rates are given as the ratio of seedling to seed. Soil moisture conditions during the cultivation are as in the following: M, moist conditions in which the soil moisture was changed from 80 to 50% of the maximum water-holding capacity; D, dry conditions, from 80 to 20%. Localities are as in Figs. 1 and 2.

Species	Seed weight	Seedling weight		Relative growth rate		Ratio of D to M
		M	D	M	D	
H. sieboldiana	2.6	51.3	37.5	19.7	14.4	0.73
H. kiyosumiensis	2.8	48.7	34.2	17.4	12.2	0.70
H. kikutii	1.2	15.7	12.5	13.1	10.4	0.80
H. pycnophylla	1.5	17.7	14.9	11.8	9.9	0.84
H. hypoleuca	1.4	21.7	16.3	15.5	11.6	0.75
H. longipes	1.8	25.6	18.7	14.2	10.4	0.73
H. albomarginata	2.8	54.5	30.5	19.5	10.9	0.56
H. longissima	2.7	40.5	16.7	15.0	6.2	0.41
H. tsushimensis	2.6	43.2	31.9	16.6	12.3	0.74
H. tibai	1.5	19.5	15.6	13.0	10.4	0.80
H. shikokiana	1.8	22.5	16.3	12.5	9.1	0.72
H. capitata	4.3	50.0	24.0	11.6	5.6	0.48

Table 4. A list of 12 species of Hosta classified into four groups as to water economic characteristics and habitat range. High, median and low magnitudes in each parameter are indicated by +++, ++ and +, respectively. Transpiration rates and growth rates were measured under moist soil conditions.

Group	Transpiration rate	Drought resistance	Growth rate	Habitat range
H. sieboldiana H. kiyosumiensis H. albomarginata H. tsushimensis	++	++	+++	+++
H. kikutii H. pycnophylla H. hypoleuca H. longipes H. tibai H. shikokiana	+	+++	+	+
H. longissima	+++	+	++	+
H. capitata	+	+	+	+

Fig 1 前田 昇

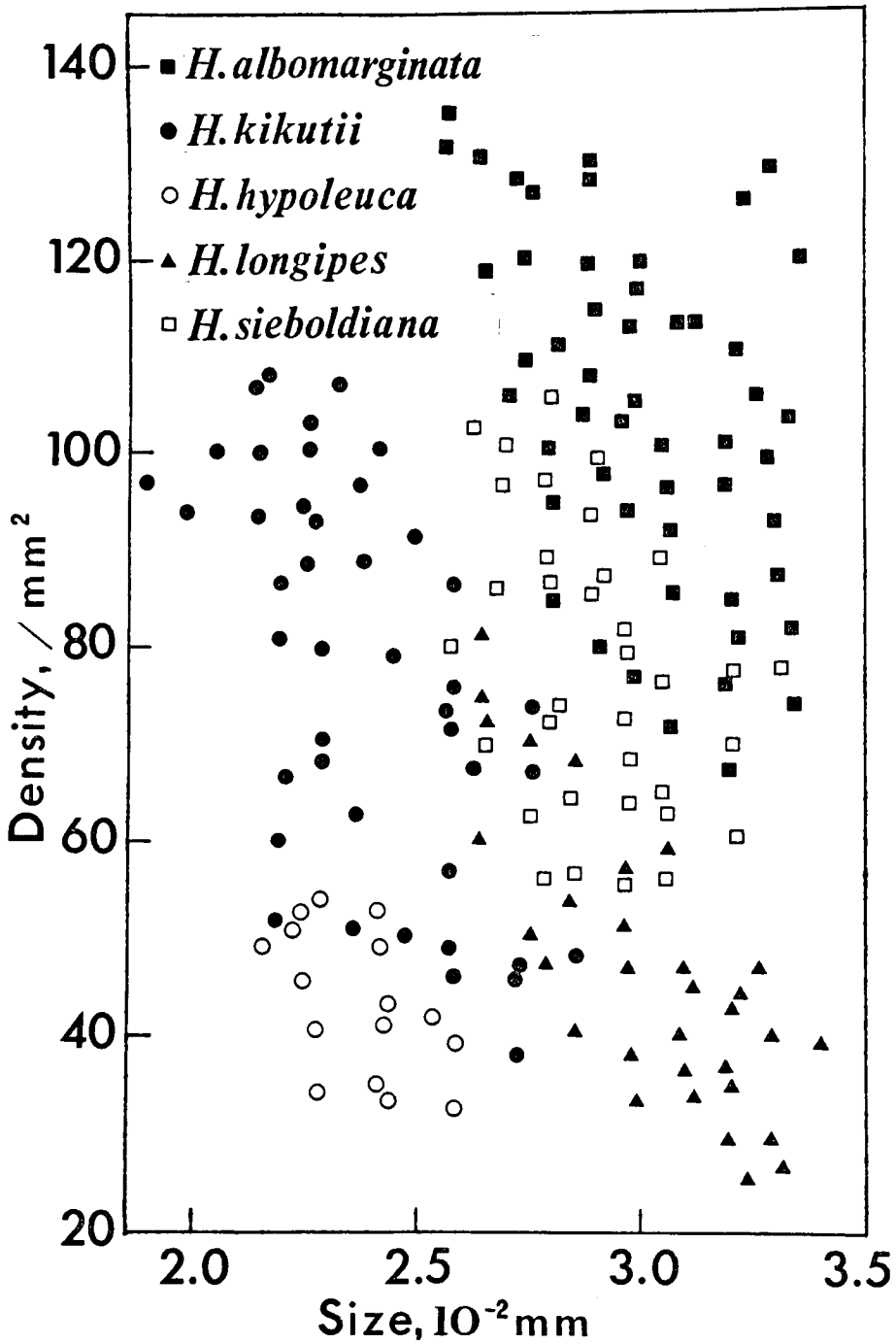

H. albomarginata
H. kikutii
H. hypoleuca
H. longipes
H. sieboldiana
140
120
100
80
60
40
20
Density, / mm²
2.0
2.5
3.0
3.5
Size, 10⁻² mm

Fig. 2 (続き)

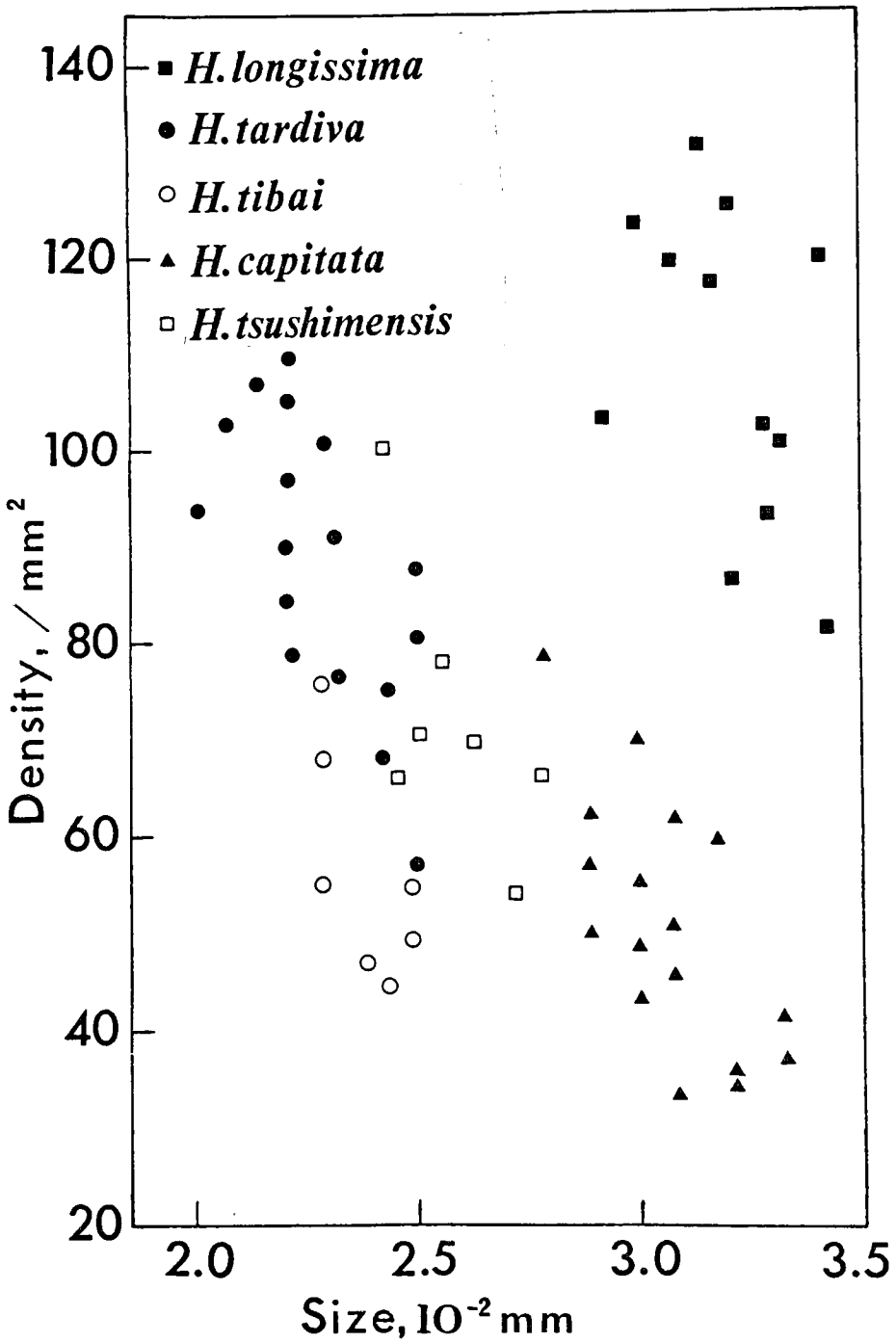

H. longissima
H. tardiva
H. tibai
H. capitata
H. tsushimensis
140
120
100
80
60
40
20
Density, / mm²
2.0
2.5
3.0
3.5
Size, 10⁻² mm

Fig 3 前の頁

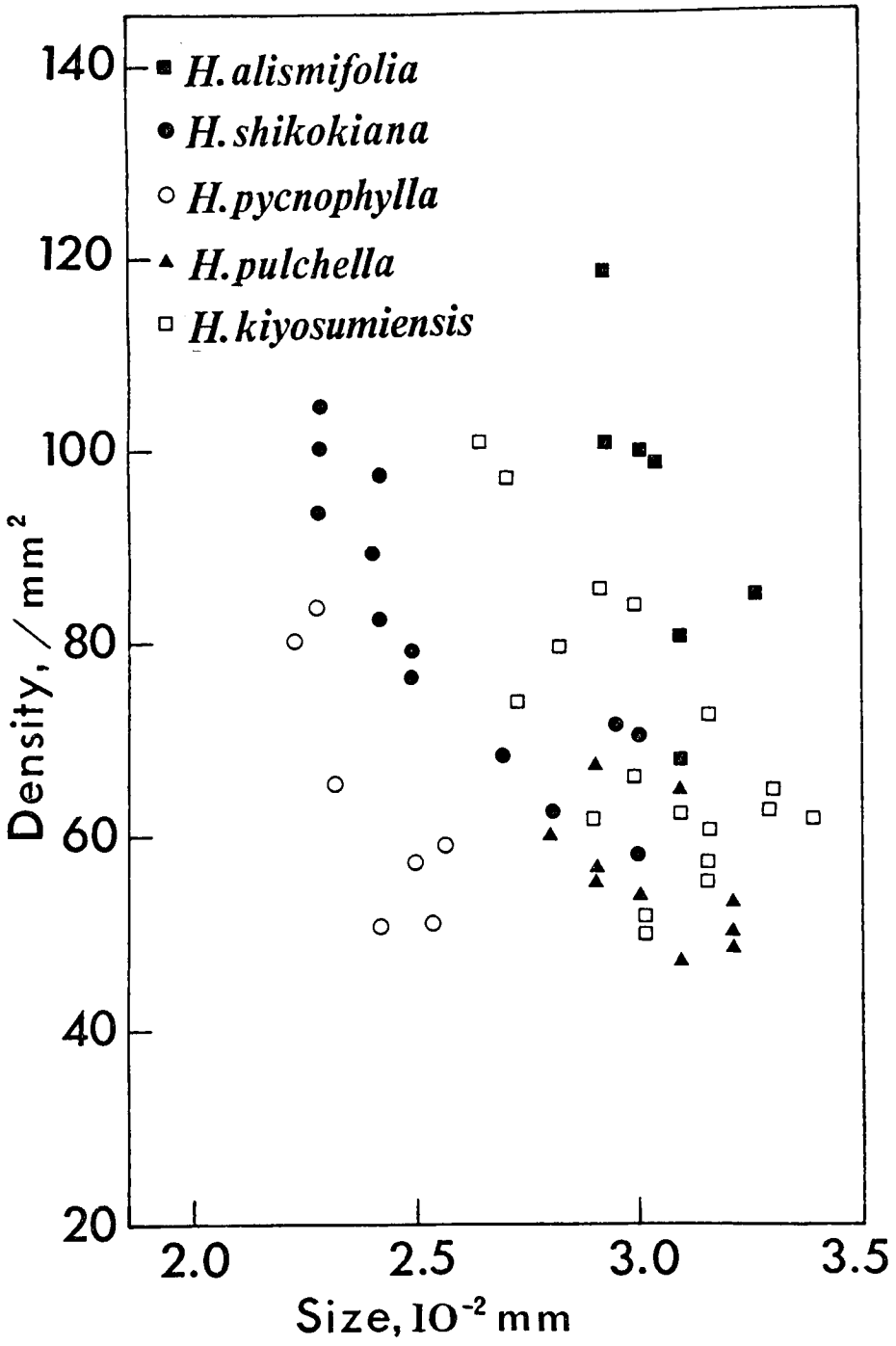

H. alismifolia
H. shikokiana
H. pycnophylla
H. pulchella
H. kiyosumiensis
140
120
100
80
60
40
20
Density, / mm²
2.0
2.5
3.0
3.5
Size, 10⁻² mm

Fig 4 藤田昇

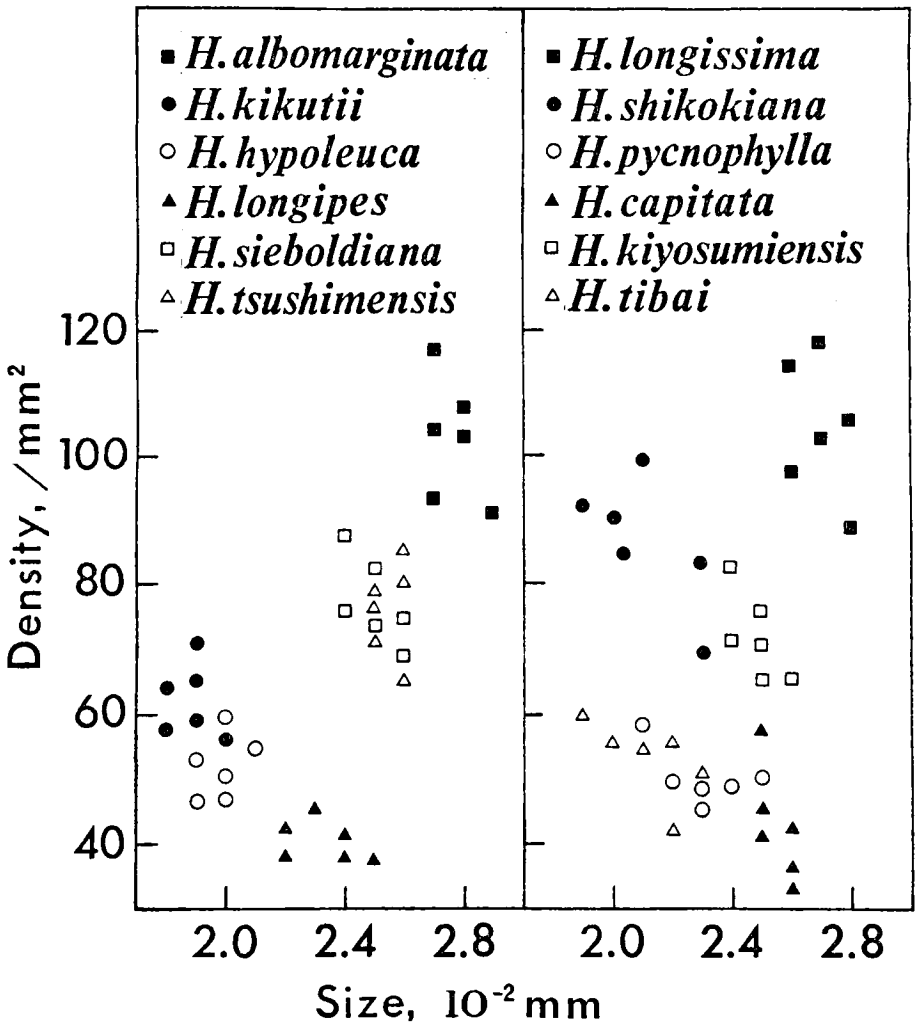

■ H. albomarginata
● H. kikutii
○ H. hypoleuca
▲ H. longipes
□ H. sieboldiana
△ H. tsushimensis
■ H. longissima
● H. shikokiana
○ H. pycnophylla
▲ H. capitata
□ H. kiyosumiensis
△ H. tibai
Density, /mm²
120
100
80
60
40
2.0
2.4
2.8
2.0
2.4
2.8
Size, 10⁻² mm

Fig.5 藤田昇

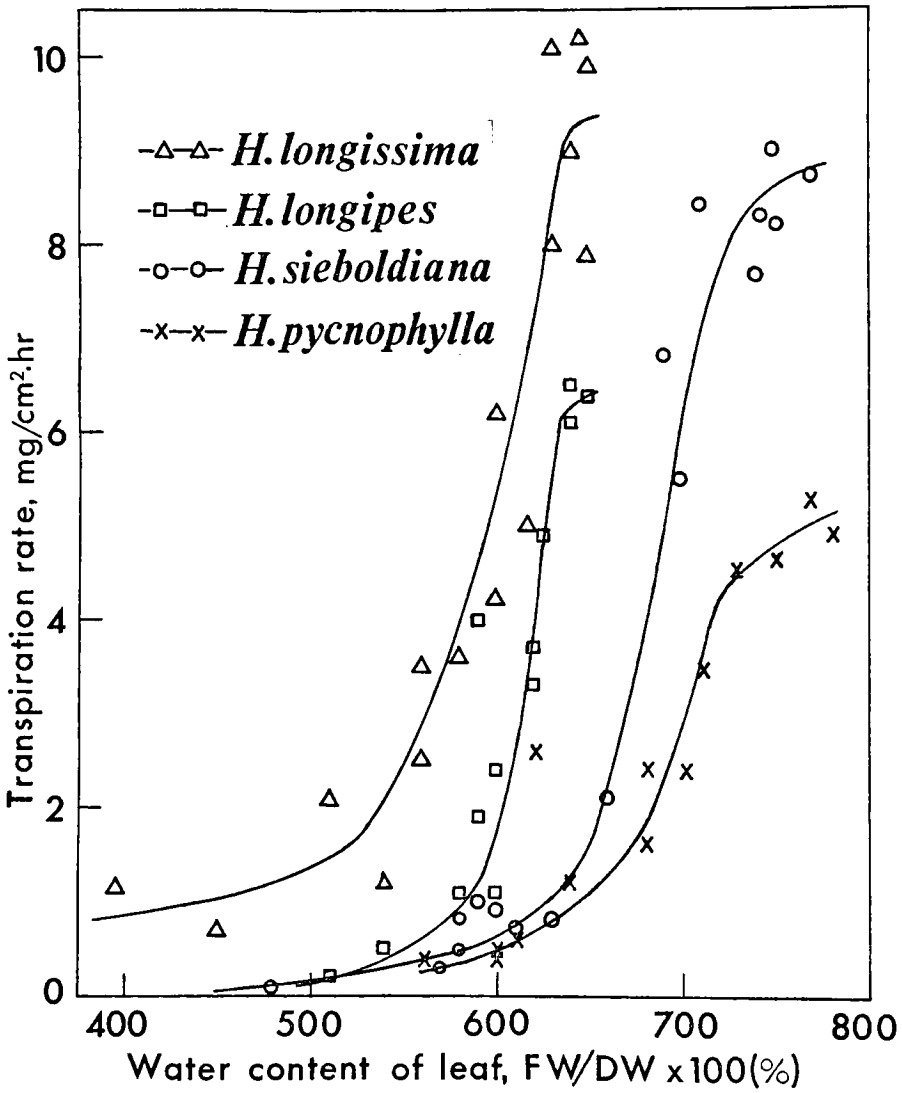

H. longissima
H. longipes
H. sieboldiana
H. pycnophylla
Transpiration rate, mg/cm².hr
Water content of leaf, FW/DW x100(%)
0
2
4
6
8
10
400
500
600
700
800

Fig 6 藤田 昇

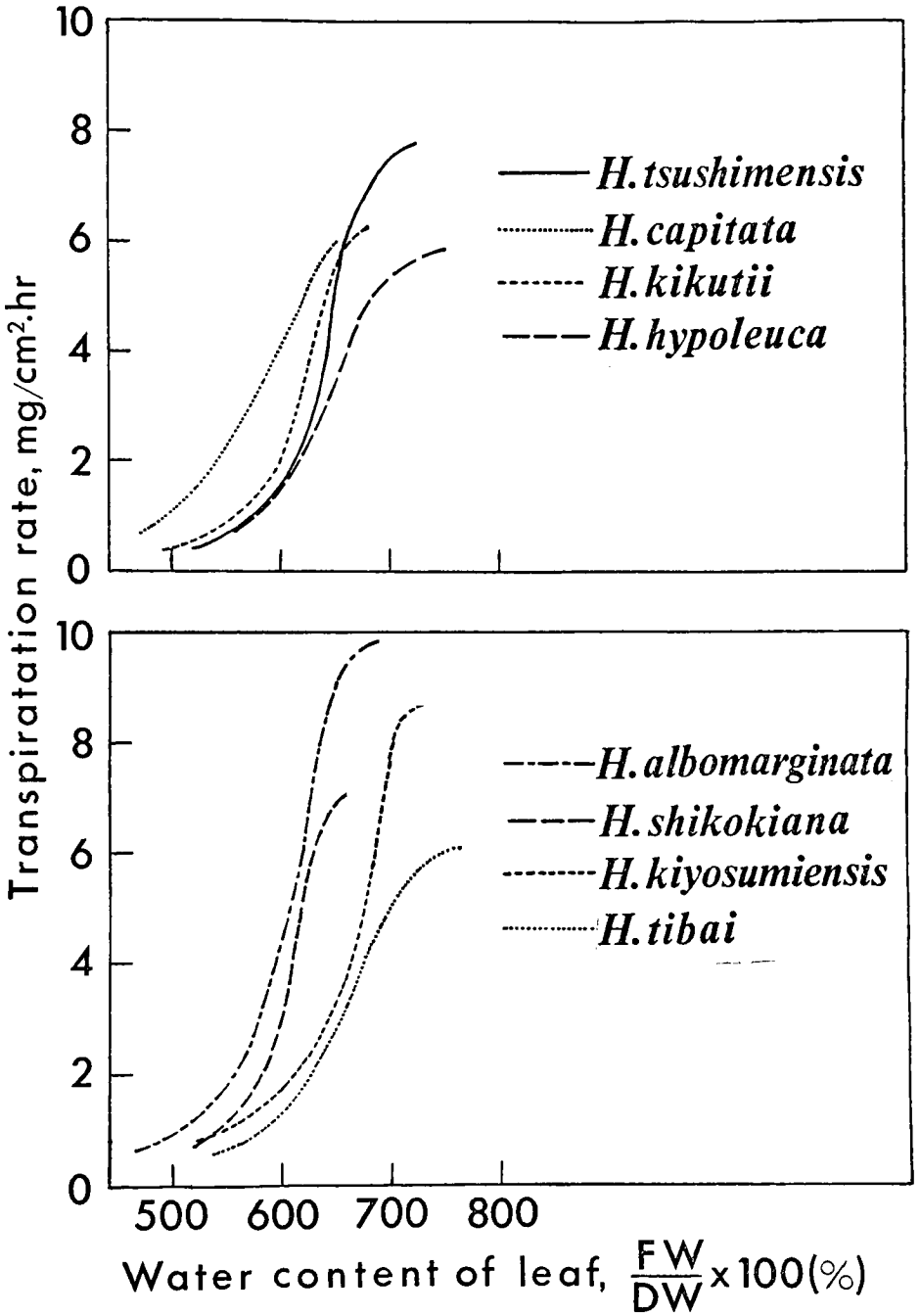

10
8
6
4
2
0
Transpiratation rate, mg/cm².hr
H. tsushimensis
H. capitata
H. kikutii
H. hypoleuca
10
8
6
4
2
0
H. albomarginata
H. shikokiana
H. kiyosumiensis
H. tibai
500
600
700
800
Water content of leaf, FW/DW x 100(%)

Fig 7 陳田昇

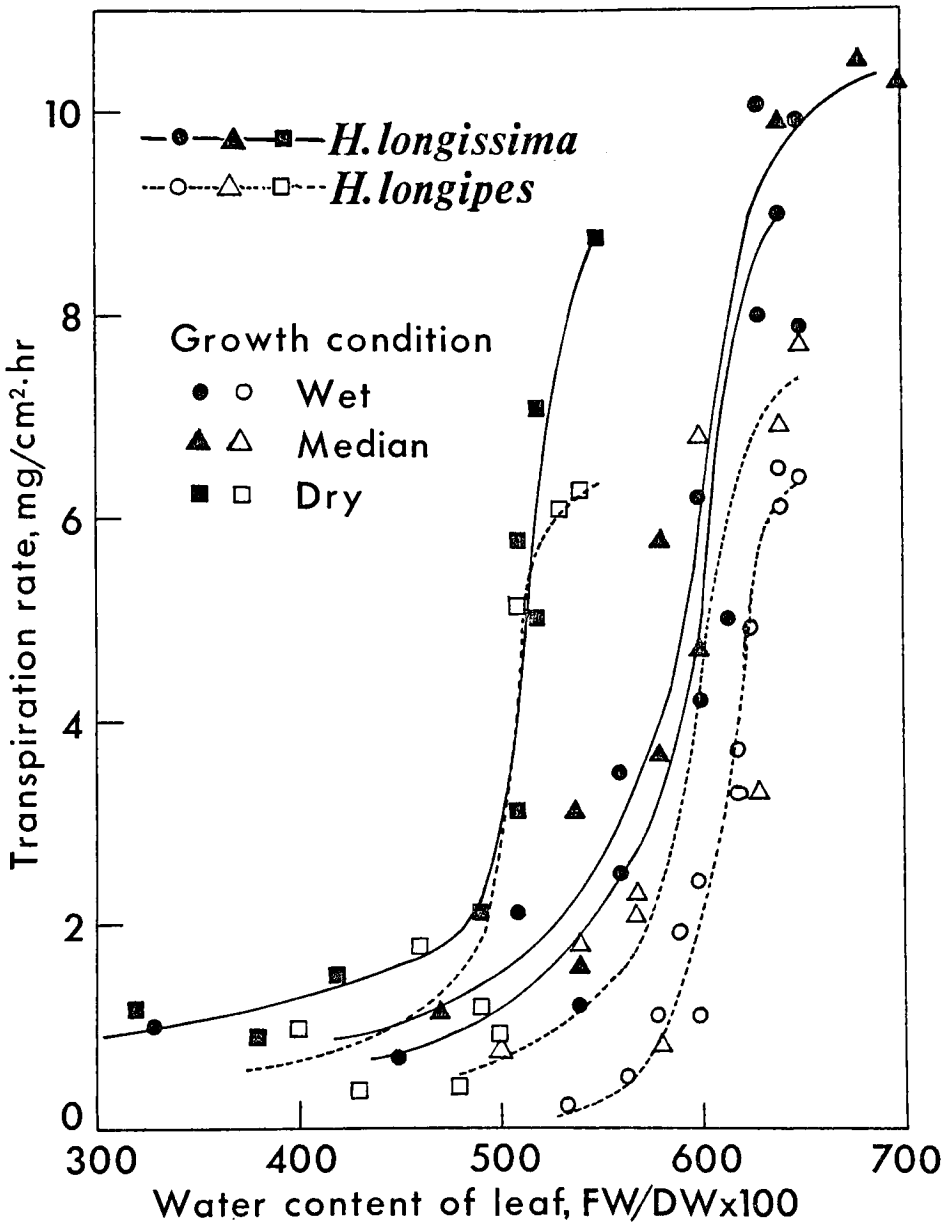

H. longissima
H. longipes
Growth condition
Wet
Median
Dry
Transpiration rate, mg/cm².hr
Water content of leaf, FW/DWx100
0
2
4
6
8
10
300
400
500
600
700

Fig 8 [illegible]

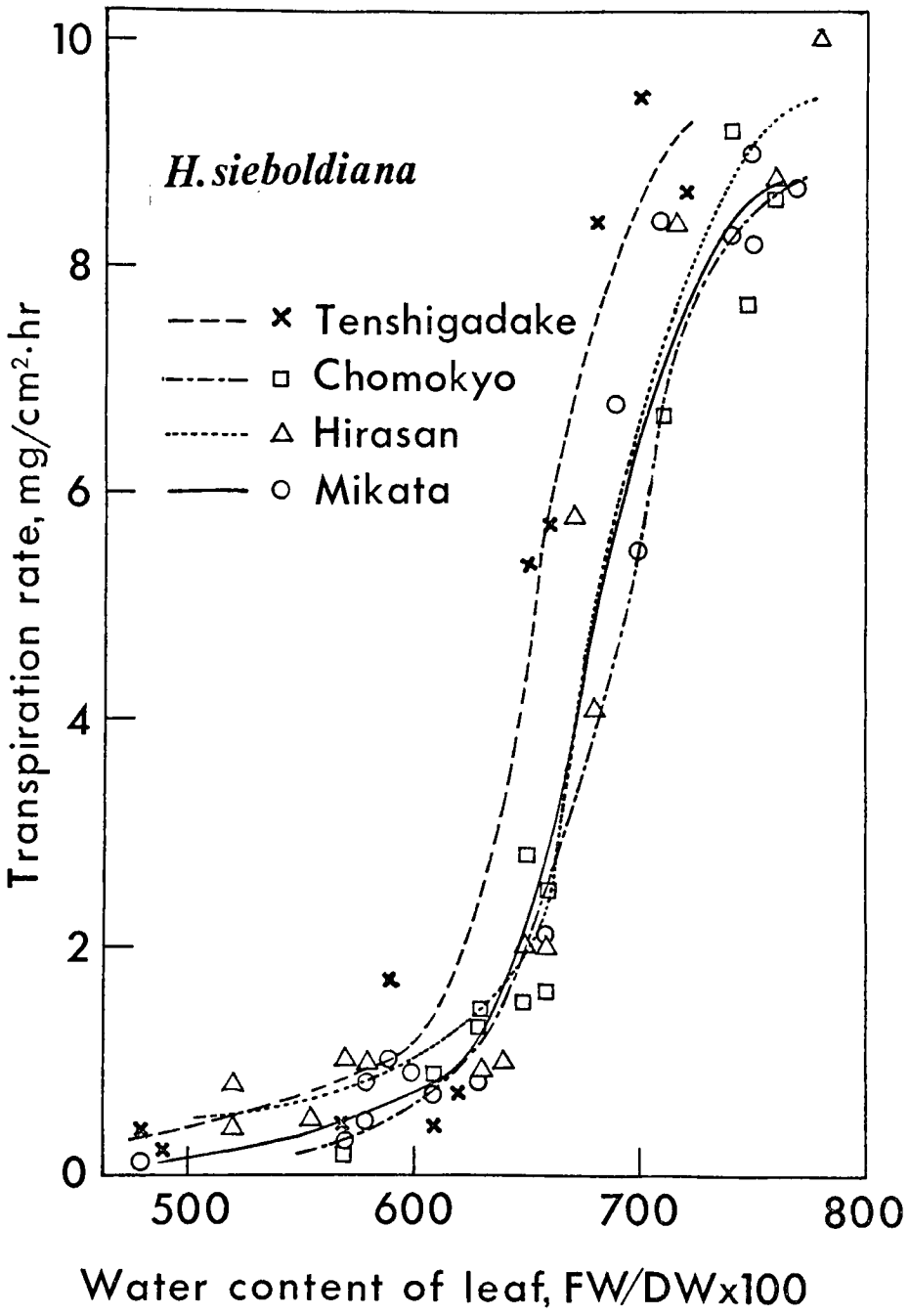

H. sieboldiana
Tenshigadake
Chomokyo
Hirasan
Mikata
Transpiration rate, mg/cm²·hr
0
2
4
6
8
10
500
600
700
800
Water content of leaf, FW/DWx100

Fig 9

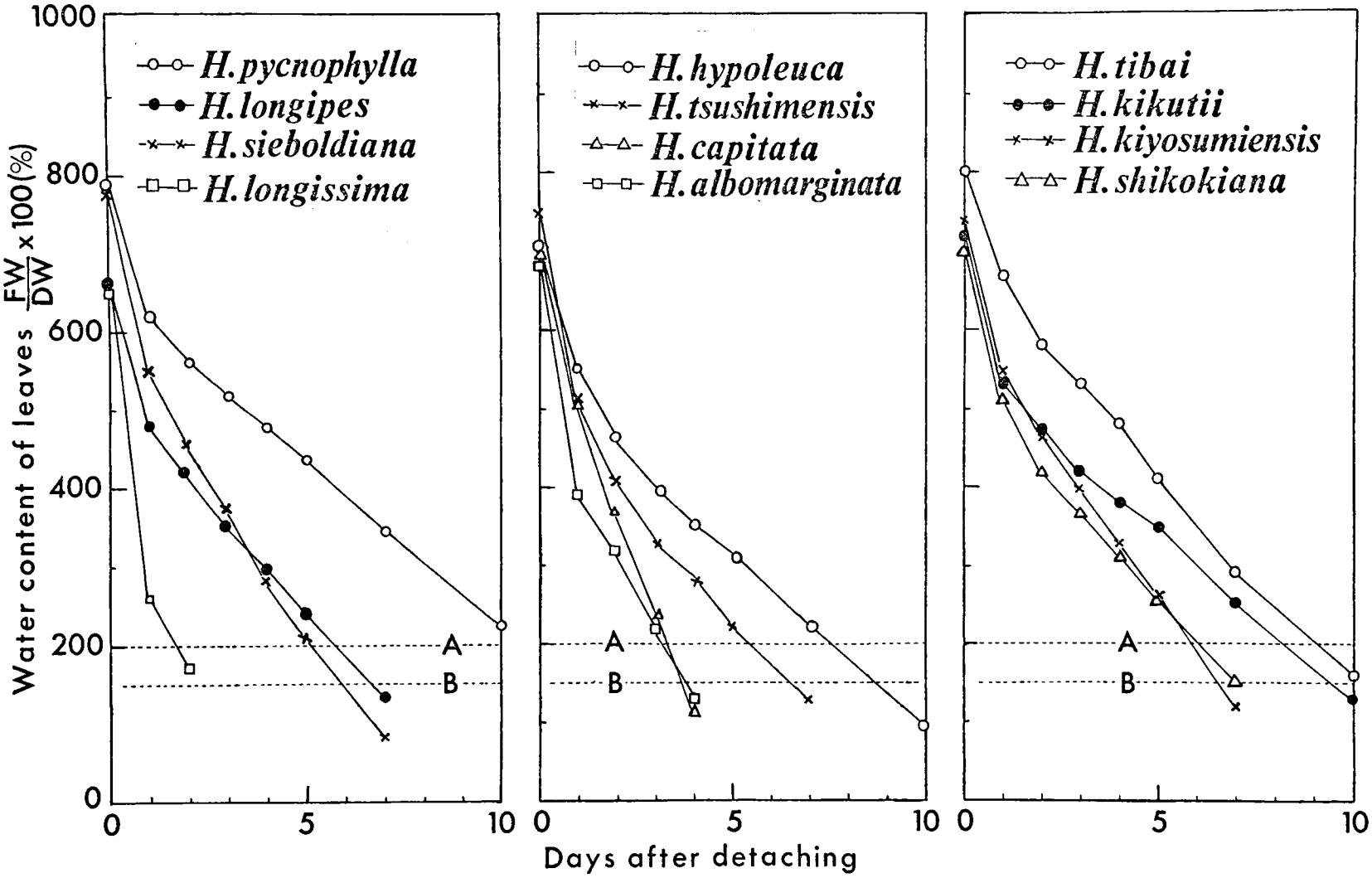
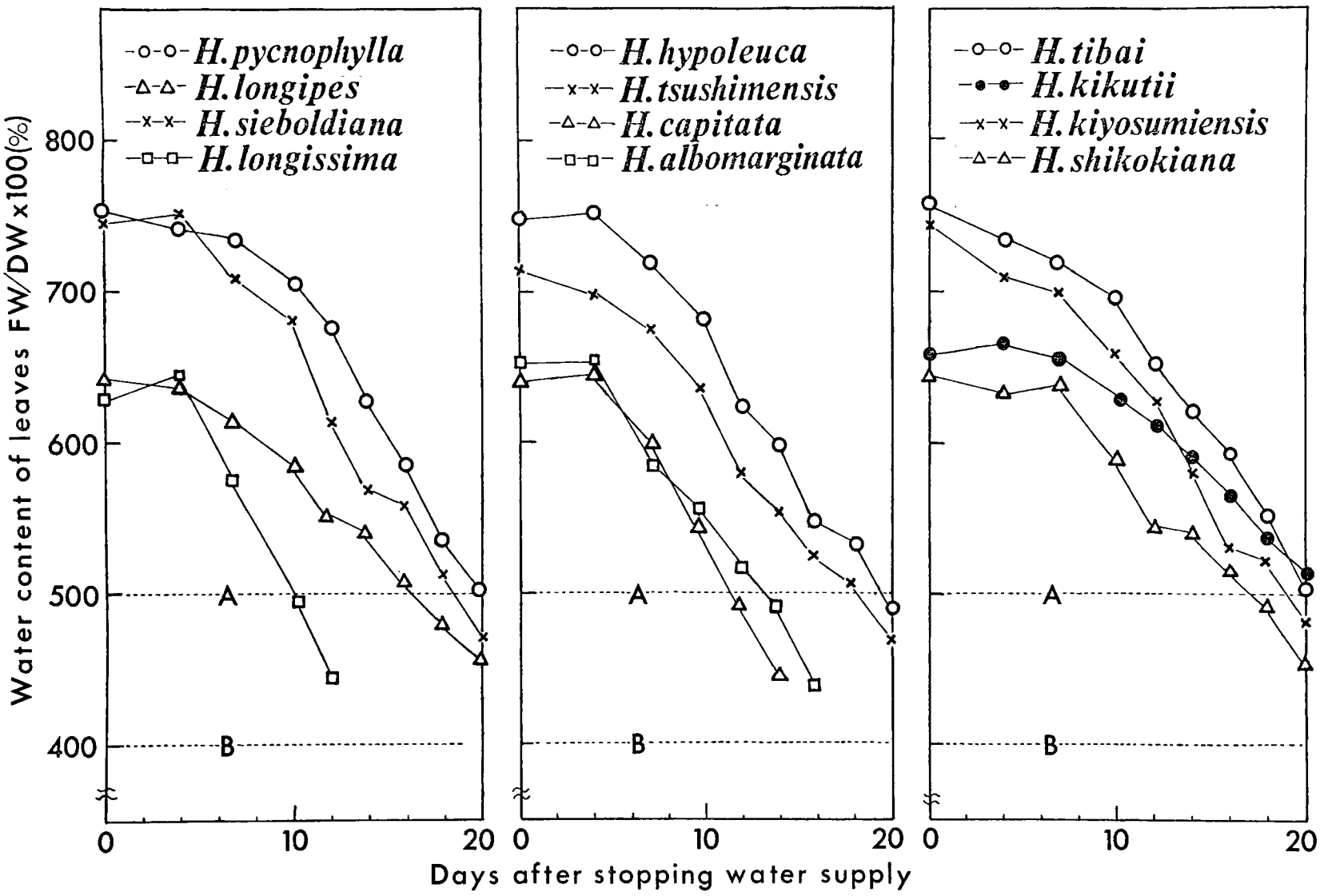

H. pycnophylla
H. longipes
H. sieboldiana
H. longissima
H. hypoleuca
H. tsushimensis
H. capitata
H. albomarginata
H. tibai
H. kikutii
H. kiyosumiensis
H. shikokiana
A
B
Water content of leaves FW/DW x 100(%)
Days after detaching
0
200
400
600
800
1000
0
5
10

Fig 10


H. pycnophylla
H. longipes
H. sieboldiana
H. longissima
H. hypoleuca
H. tsushimensis
H. capitata
H. albomarginata
H. tibai
H. kikutii
H. kiyosumiensis
H. shikokiana
Water content of leaves FW/DW x100(%)
800
700
600
500
400
A
B
0
10
20
Days after stopping water supply

FLOODING TOLERANCE OF JAPANESE HOSTA IN RELATION TO HABITAT PREFERENCE

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Introduction

In the previous paper (Fujita, 1976b) reported was the transpiration rate and the drought resistance of the Japanese species of Hosta in relation to the habitat preference. Their water economic characteristices have mainly to do with the adaptition to dry habitats. Hosta species are, however, found in various habitats, and their soil moisture conditions are diverse from excessively wet to relatively dry. For the understanding of physiological adaptation to the soil moisture conditions of the habitats, it is also necessary to know how each Hosta species responds to wet conditions.

Flooding brings about poor aeration and consequently reduced conditions in soaked soil. When the soil containing organic debris is flooded with water, the soil becomes deficient in oxygen and the organic debris is decomposed by microbes. The redox-potencials of the soil lowers, and the reduced products, such as S^{--}, Fe^{++} and Mn^{++}, which affect harmfully plant roots, are then produced in the soil(Robinson, 1930; Sato and Yamane, 1960). In order to inhabit wet places healthy, plants must be able to withstand anoxia and to counteract toxic reduced products. Respiratory metabolism and oxidizing power in flooded plant parts, therefore, come into question.

There have been some reports as to this question. Helophytes had metabolic adaptation to anaerobic environments, avoiding excess ethanol accumulation(Crawford, 1966 and 1967; Crawford and McManmon, 1968; Crawford and Tyler, 1969; Tyler and Crawford,

1970). Rice seedlings were found to be more tolerant of ethanol than wheat or oat seedlings from growth studies(Taylor, 1942; Nagao and Ohwaki, 1953). Swamp plants were more resistant to strongly reduced soil conditions than upland plants(Yamasaki, 1952; Doi, 1952).

In this paper flooding tolerance, and respiratory metabolism and oxidizing power of roots in Japanese species of Hosta are determined and relationships between their characteristics and habitat preference of species are compared from the viewpoint of adaptation and ecology.

Materials and Methods

For experiments used were all the species of Japanese Hosta, which is 15 species according to Fujita(1976a).

All the plants examined were collected from native habitats. The rhizomes with winter buds were planted and grown in pots in the greenhouse from February to May in 1974, where air temperature was maintained to higher than 17°C. In 6:3:2 volume ratio, the soil in the pots consisted of sandy loam, humus and small stone which had ca. 5 mm diameter. The soil moisture was regulated to be constant at 60-50% based on the maximum water-holding capacity which was 42% in the basis of dry weight when dried for 5 days at 105°C. New leaves and roots were developed during the cultivation.

Flooding experiments were started about 50 days after the planting. Pots with plants of each species were flooded with water so that only roots of the plants might be fully soaked. Flooding tolerance of each species was determined after 40 days' flooding.

Plants of which roots preserved their health were judged to be flood-tolerant, and plants of which roots were spoiled were regarded as flood-intolerant.

The respiratory and oxidative activities were measured after 10-14 days' flooding. It was shown that the high alcohol dehydrogenase activity in roots of non-helophytes was induced after 5 day' flooding(Crawford and McManmon, 1968). The duration of flooding in the experiments was long enough to induce metabolic changes, if any, and besides the duration was determined to avoid the occurrence of damping of flooded plant roots during the flooding treatments. Roots were cut off from plants and cleansed by water. After being rinsed for 2 min in 0.02% $HgCl_2$ solution, they were washed throughly with deionized water to minimize bacterial contamination. Then apical roots of 5 cm long were cut into 3 mm sections with a multiple razor blade cutter, followed by blotting and weighing. Only new roots which had developed after the planting were used for measurements to eliminate age differences in activities.

Oxygen uptake in aerobic respiration was determined by the Warburg manometry. For each Warburg flask 15-17 ml in volume, 0.2 g of root sections or leaf disks were suspended in 1.3 ml of M/15 phosphate buffer, pH 6.0. CO_2 output in anaerobic respiration was measured by subsequently gassing with nitrogen those flasks which contained 0.2 ml of the buffer instead of 0.2 ml of 20% KOH solution in the center well. The flasks were shaken at 30° C in the dark. R. Q. was determined accoding to Warburg's direct method, using 0.1 M citric acid-0.2 M Na_2HPO_4 solution at pH 4.8.

Oxidative activity of the roots was measured by α-naphtylamine oxidation, for it was reported that the roots which stained

distinctly in α-naphtylamine solution had high oxidizing power in paddy field conditions(Doi, 1952) and quantitative analysis of α-naphtylamine was possible(Sakai and Yoshida, 1957). Apical roots of about 5 cm long and of approvimately i g in frsh weight were placed in a test tube which contained 8 ml of M/15 phosphate buffer(pH 6.0) and 1 ml of 180 ppm α-naphtylamine solution. The tubes were then placed in an incubator and were shaken for 6 hr in th dark at 37° C, and the reaction was stopped by the addition of 1 ml of 50% acetic acid. As cotrols, similar samples without root sections were treated alike to exclude the automatic oxidation of α-naphtylamine from the measured value of oxidation. A quantitative estimation of α-naphtylamine was conformable to Griess' method. To 3 ml of 1% sulphanilic acid solution in 30% acetic acid added was 4 ml of 100 ppm KNO_2 solution in a measuring flask 10 ml in volume, and the flask was shaken and left for several min. at room temperature. A 1 ml aliquote of the sample and 2 ml of deionized water were then added into the flask, and the flask was shaken repeatedly and left at room temperature for about 5 min. The absorptimetry was carried out at 520 mμ with a spectrophotometer.

After the measurements of respiratory and oxidative activities, the sections and disks were dried for 2 days at 95° C and dry weight was determined.

In parallel with these experiments, seedling growth was determined under sand culture conditions in order to examine effects of soil organic matters on flooding tolerance of plants. Seeds were sown in potts at 5 mm depth in sand whose water capacity was 16% on dry weight base under one of the follwing two water table conditions: (1) high water table, maintaining water surface

1 cm below the sand surface; and (2) low water table, 15 cm below. The pots were made not to be exposed to the rain with vinyl cover. After the growth of one season, seedlings of each species were harvested and their biomass was determined.

Results

Flooding Tolerance

In Table 1 shown are flooding tolerance and habitat preference of *Hosta* species examined. The species occurring in wet places are more tolerant of flooding than the other species, showing rather good growth under the flooding conditions. Those which grow in various habitats have adequate tolerance in spite of slightly retarded growth, retaining healthy roots throughout the flooding duration. Those restricted on outcrops are so highly susceptible to flooding as to get their roots decayed. *H. tibai*, *H. capitata*, *H. tardiva* and *H. pycnophylla* also show low tolerance, being found on rocky soils as well as outcrops.

Respiratory Activities

Table 2 represents aerobic respiration rates for roots from the flooding and non-flooding conditions. There were little interspecific differences in O_2 consumption among the plants grown under non-flooding conditions. Under the flooding conditions, the plants of flood-intolerant species exhibited a slight tendency to reduce the rates of O_2 uptake in comparison with those under the flooding conditions.

In Table 3 recorded are anaerobic respiration rates for roots from the flooding and non-flooding conditions. Between the plants resistant to flooding and those intolerant of it found were no differences in the values of the ratios.

Oxidative Activities

In Table 4 summarized is oxidation of α-naphtylamine by roots. Good correlation is found between the ability to oxidize α-naphtylamine and the level of flooding tolerance. After the flooding treatments the oxidative activities for roots fell in the flood-unresistant plants, while it remained unchanged in flood-tolerant ones. The roots of the plants which did not stand up to flooded soil conditions revealed adequate tolerance in the case of water culture, not decresing the oxidizing power.

Intraspecific Variation

When fluctuation of flooding tolerance within a species is considerable, interspecific comparison may lose its meaning. It is, therefore, necessary to investigate the range of intraspecific variation in flooding tolerance. In H. sieboldiana having the most various habitats among the Hosta species, examined was intraspecific variation due to differences in the habitats from which the rhizomes were collected for the experiments. It was shown that intraspecific variation was small enough(Table 5).

Seedling Growth

Seedling growth and survival under different water table conditions are shown in Table 6. Under the condition of sand culture which does not contain soil organic matter, the species which are highly susceptible to flooding when grown in the soil with organic debris do not necessarily show ill growth compared with those which grow in wet habitats. In contrast, the latter species are less resistant to flooding in sand culture.

Discussion

Plants from wet places have been expected to demand smaller

O_2 supply than plants from dry areas. It was reported that O_2 consumption was low in plants growing in those habitats that gived ground water of low dissolved O_2 concentration(Hogetsu et al., 1954), while no distinct differences were found in aerobic respiration rates between plants from wet habitats and those from dry regions(Crawford, 1966). In Hosta there were little interspecific differences in the rates of O_2 uptake.

According to Crawford(1966), flooding induced and increased rate of anaerobic CO_2 evolution in the roots of flood-unresistant plants, while plants tolerant of flooding showed little changes in a rate of CO_2 evolution when flooded. The acceleration of glycolysis resulted in accumulating toxic concentration of ethanol under hypoxic conditions in flood-intolerant plants. It was reported that flood-tolerant plants seemed to have some alternative metabolic pathways which enable them to stand up better to anaerobic environments(Crawford and McManmon, 1968; Crawford and Tyler, 1969; Tyler and Crawford, 1970). In the present experiments, however, such metabolic changes were not discovered in Hosta roots, for alcoholic fermentation activities seemed not to rise under the flooded soil conditions in flood-unresistant species, judging from the rates of anaerobic CO_2 output.

As far as the present measurements are concerned, it may be safely said that the level of flooding tolerance is closely associated with the power of α-naphtylamine oxidation by roots under steeped soil conditions. The resistance to reduced soil conditions plays an inportant part in flooding tolerance. But metabolic base of oxidative activities has not been made clear, though it was presumed that α-naphtylamine oxidation was brought

about by coupling enzyme system producing H_2O_2 in the peroxidase system(Sakai and Yoshida, 1957). In flooded roots of flood-intolerant Hosta species, lowering of oxidation had a tendency to be accompanied with slight decrease of O_2 uptake rates.

Under non reduced soil conditions the above-mentioned flood-unresistnt species are not necessarily less resistant to flooding than the species which have high resistnce to flooding under reduced soil conditions. This also suggest that the oxidizing capacity is important in flooding tolerance. The Hosta species which inhabit wet places show retarded growth under flooded conditions of non-reduced soil, as seen in rice plant(Takagi, 1966).

Flooding tolerance is one of the important features playing important role in determining the habitats range in Hosta species, in connection with drought resistance examined in the previous paper. According to hydrophysiological viewpoints, Hosta species may be classified into the following 4 groups: namely, (1) the species showing high flooding tolerance and low drought resistance, and occurring in wet habitats: H. longissima, H. albo-marginata, and H. alismifolia, (2) those exhibiting high drought resistance and low flooding tolerance, and being confined on outcrops and in fairly dry places: H. tardiva, H. tibai, H. kikutii, H. pycnophylla, H. hypoleuca, H. longipes, H. pulchella, and H. shikokiana, (3) the species which have low resistance to both flooding and drought, and being found mostly in somewhat peculiar habitats with serpentine or limestone; H. capitata, (4) those bearing fairly high tolerance to both flooding and drought, and having wide habitat ranges as to the soil moisture; H. sieboldiana, H. kiyosumiensis and H. tsushimensis.

Though the first and second groups mostly stand up higher to flooding or drought respectively than the fourth group, they are restricted to narrow habitat range as a result of strict adaptation to definite soil moisture conditions, As against them, the species thriving vigorously in various habitats possess physiologically flexible adaptability to changeable soil moisture conditions.

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I am also indebted to Mr S. Tomida and Mr I. Kojima for their aids to grow the plants.

Summary

1) Fifteen species of Japanese *Hosta* were compared each other in flooding tolerance, respiratory metabolism and oxidizing power in relation to habitat preference from the viewpont of adaptation.

2) The species inhabiting wet places had very high resistance to flooding. Those growing in various habitats bore adequate tolerance. In those restricted on outcrops and in fairly dry places, on the other hand, high susceptibility was found.

3) Between flood-tolerant plants and flood-unresistant plants, there were little differences in aerobic and anaerobic respiration rates under flooding and non-flooding conditions.

4) Good correlation was found between the ability to oxidize α-naphtylamine and the degree of flooding tolerance. Those species that did not withstand flooding showed the lowering of oxidative activities in flooded roots, while the oxidizing power remained unchanged in flooded roots of flood-resistant species.

5) It was shown that flooding tolerance was one of the features playing important part in determining the habitat ranges in *Hosta* species.

Table 1. Habitat preference and flooding tolerance of the species. ++, high tolerance with good growth; +, adequate tolerance with healthy roots and slightly retarded growth; ±, low tolerance with partially damping roots; -, high susceptibility to flooding with fully damping roots.

Species	Flooding tolerance	Habitat
H. albo-marginata	++	wet places in the most
H. longissima	++	low moor
H. alismifolia	++	low moor
H. sieboldiana	+	various habitats
H. kiyosumiensis	+	various habitats
H. tashimensis	±	fairly various habitats
H. tardiva	±	country roadside
H. tibai	±	outcrops and mountain path-sid
H. kikutii	±	outcrops
H. hypoleuca	±	outcrops
H. pulchella	±	outcrops
H. capitata	-	outcrops and mountain path-sid
H. pycnophylla	-	fairly dry ridge
H. longipes	-	outcrops
H. shikokiana	-	outcrops

Table 2. Aerobic respiration rates (Qo_2) in µl O_2 uptake/h/mg dry weight of roots. Each figure shows the mean value with its standard deviation. The number of replicates is given in parentheses. N, un-flooded roots from moist soil conditions; F, flooded roots from soaked soil conditions; W, water-logged roots.

Species	N	F	W	Ratio N : F : W
H. albo-marginata	1.21 ±0.02(2)	1.37 ±0.10(3)	1.09 ±0.11(2)	1 : 1.13 : 0.90
H. longissima	1.33 ±0.02(3)	1.21 ±0.01(2)	1.84 ±0.11	1 : 0.91 : 1.38
H. alismifolia	1.41 ±0.13(3)	1.05 ±0.07(3)	——	1 : 0.74 ——
H. sieboldiana	1.03 ±0.05(3)	1.28 ±0.06(3)	1.16 ±0.10(2)	1 : 1.24 : 1.13
H. kiyosumiensis	1.00 ±0.08(3)	1.09 ±0.12(3)	——	1 : 1.09 ——
H. tsushimensis	1.31 ±0.04(3)	0.92 ±0.10(3)	——	1 : 0.70 ——
H. tardiva	1.15 ±0.04(2)	0.88 ±0.03(2)	——	1 : 0.77 ——
H. tibai	1.36 ±0.05(3)	1.13 ±0.02(3)	——	1 : 0.83 ——
H. kikutii	1.24 ±0.04(2)	1.03 ±0.05(2)	——	1 : 0.88
H. hypoleuca	1.33 ±0.06(2)	1.08 ±0.12(2)	——	1 : 0.81 ——
H. pulchella	1.09 ±0.05(2)	0.98 ±0.12(2)	——	1 : 0.90 ——
H. capitata	1.12 ±0.13(3)	0.67 ±0.10(3)	0.99 ±0.04(2)	1 : 0.60 : 0.89
H. pycnophylla	1.12 ±0.03(3)	0.76 ±0.01(3)	0.96 ±0.13(2)	1 : 0.68 : 0.86
H. longipes	1.05 ±0.01(3)	0.84 ±0.02(3)	1.16 ±0.03(2)	1 : 0.80 : 1.10
H. shikokiana	0.85 ±0.05(3)	0.80 ±0.02(3)	——	1 : 0.94 ——

Table 3. Anaerobic respiration rates ($Qco_2 \underline{n}_2$) in µl CO_2 output/ h/mg dry weight of roots. Notes as Table 2.

Species	N	F	W	Ratio N : F : W
H. slbo-marginata	0.86 ±0.01(2)	1.09 ±0.09(3)	0.93 ±0.01(2)	1 : 1.27 : 1.08
H. longissima	1.08 ±0.07(3)	0.86 ±0.03(3)	1.24 ±0.03(2)	1 : 0.80 : 1.20
H. alismifloia	0.98 ±0.05(3)	0.82 ±0.10(3)	——	1 : 1.06 ——
H. sieboldiana	0.66 ±0.06(3)	0.96 ±0.10(3)	1.24 ±0.05(2)	1 : 1.46 : 1.87
H. kiyosumiensis	0.83 ±0.01(3)	0.74 ±0.02(3)	——	1 : 0.89 ——
H. tsushimensis	0.83 ±0.10(3)	0.84 ±0.02(3)	——	1 : 1.01 ——
H. tardiva	0.84 ±0.03(3)	0.57 ±0.03(3)	——	1 : 0.68 ——
H. tibai	0.45 ±0.02(3)	0.90 ±0.03(3)	——	1 : 2.00 ——
H. kikutii	0.92 ±0.02(2)	0.67 ±0.06(2)	——	1 : 0.73 ——
H. hypoleuca	0.89 ±0.07(2)	1.03 ±0.07(2)	——	1 : 1.16 ——
H. pulchella	0.68 ±0.02(2)	0.73 ±0.10(2)	——	1 : 1.07 ——
H. capitata	0.83 ±0.04(2)	0.47 ±0.06(3)	0.87 ±0.08(2)	1 : 0.57 : 1.05
H. pycnophylla	0.72 ±0.11(3)	1.02 ±0.04(3)	0.92 ±0.00(2)	1 : 1.42 : 1.28
H. longipes	0.74 ±0.02(3)	0.86 ±0.08(3)	0.60 ±0.00(2)	1 : 1.16 : 0.81
H. shikokiana	0.55 ±0.04(3)	0.47 ±0.03(3)	——	1 : 0.85 ——

Table 4. Oxidation of α-naphtylamine in mg/6h/g dry weight of roots. Each figure represents the mean value of two experiments. Symbols as in Table 2.

Species	N	F	W	Ratio N : F : W
H. albo-marginata	0.48	0.48	0.48	1 : 1.00 : 1.00
H. longissima	0.55	0.55	0.61	1 : 1.00 : 1.11
H. alismifolia	0.45	0.41	——	1 : 0.91 ——
H. sieboldiana	0.61	0.59	0.50	1 : 0.97 : 0.82
H. kiyosumiensis	0.59	0.57	——	1 : 0.97 ——
H. tsushimensis	0.47	0.31	——	1 : 0.66 ——
H. tardiva	0.48	0.32	——	1 : 0.67 ——
H. tibai	0.62	0.30	——	1 : 0.48 ——
H. kikutii	0.57	0.29	——	1 : 0.51 ——
H. hypoleuca	0.74	0.31	——	1 : 0.43 ——
H. pulchella	0.58	0.25	——	1 : 0.44 ——
H. capitata	0.60	0.20	0.60	1 : 0.33 : 1.00
H. pycnophylla	0.51	0.22	0.46	1 : 0.42 : 0.90
H. longipes	0.86	0.26	0.56	1 : 0.30 : 0.65
H. shikokiana	0.63	0.29	——	1 : 0.46 ——

Table 5. Intraspecific variation of H. sieboldiana var. gigantea in flooding tolerance, and respiratory and oxidative activities owing to habitat differences. Symbols and units of the activities as in Table 2, 3 and 5. Standard deviation of each figure is omitted. Localities and habitats: Noma(Kyoto Pref.), moist place in a light forest; Mikata(Fukui Pref.), wet place in a stream bed; Chomonkyo(Yamaguchi Pref.), outcrop in a valley; Hirasan(Shiga Pref.), fairly dry mountain ridge; Uraresan(Iwate Pref.), fairly dry mountain slope in a calcareous area; Tsukude (Aichi Pref.), low moor.

Locality	Flooding tolerance	Qo_2		$Qco_2\underline{n}_2$		Oxidation	
		N	F	N	F	N	F
Noma	+	1.03(3)	1.28(3)	0.66(3)	0.96(3)	0.61	0.59
Mikata	+	1.36(3)	1.30(3)	0.86(2)	0.81(2)	0.62	0.71
Chomonkyo	+	1.23(3)	1.34(3)	0.78(3)	0.80(3)	0.47	0.34
Hirasan	+	1.45(2)	1.54(2)	1.08(2)	1.21(3)	0.60	0.54
Uraresan	+	1.04(2)	1.03(2)	0.85(2)	0.67(2)	0.59	0.53
Tsukude	+	1.15(3)	1.09(3)	0.68(2)	0.75(3)	0.49	0.48

Table 6. Seedling growth under low and high water tables in sand culture. Seedling biomass was measured in the first autumn. Each figure of biomass shows the average value of 100 seeds or all survived seedlings. Biomass is expressed in mg DW. Growth and survival ratios are given as the percentages of high water table to low water table.

Species and locality	Seed weight	Seedling weight Water table Low	High	Growth ratio	Survival ratio
H. sieboldiana Oeyama (Kyoto Pref.)	2.6	112.0	53.3	48	77
H. kiyosumiensis Asama (Mie Pref.)	3.2	135.0	40.5	30	70
H. kikutii Takakuma (Kagoshima Pref.)	1.2	66.7	21.7	33	85
H. pycnophylla Oshima (Yamaguchi Pref.)	1.5	64.2	27.3	43	76
H. hypoleuca Horai (Aichi Pref.)	1.4	37.7	15.4	41	71
H. longipes Kitakomatsu (Shiga Pref.)	1.7	92.0	26.2	28	82
H. albomarginata Ninnikusen (Nara Pref.)	2.7	105.2	24.8	24	67
H. longissima Kakogawa (Hyogo Pref.)	2.9	140.6	25.6	18	80
H. capitata Niyodo (Kochi Pref.)	4.2	167.0	43.3	26	83

主論文3

REPRODUCTIVE CAPACITY AND LEAF DEVELOPMENT OF JAPANESE HOSTA VIEWD FROM ECOLOGY AND EVOLUTION

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Introduction

Modern ecology originated with Darwin, and since then, the study on the life of species has been presented as an important problem in ecology. Darwin(1859) made it clear that the evolution of species is caused by the change of life, and that species establish their places in the economy of nature, struggling for existence and adapting themself to their environments. His method of concretely analyzing the life of species are valuable, but it is open to serious question that he regarded the competion among individuals of the same species as the severest. Afterward, it was definitely shown by Lysenko(1954) in plants, that intraspecific relationship is qualitatively different from interspecific relationship and intraspecific mutually adaptive relationship is an essential attribute. Thus, the species really exists as the basic unit of living of organisms.

In order to study the life of Japanse Hosta species from these ecological viewpoints, habitat preference and water relations in each species were investigated in previous papers(Fujita, 1976b, in prep.). Differences in adaptability of water relations were found among Hosta species. The species which commonly live in varied habitats, such as H. sieboldiana, showed broad adaptabilty to soil moisture conditions of the habitat, while those which occur in restricted habitats, for example, H. kikutii and H. longissima, displayed rigid adaptability to a particular condition.

The adaptability in reproductive process must be understood in the study on the life of any species, because successful reproduction is indispensable for the preservation of species. In addition, adaptability of species has beeb acquired in the historical process under phylogenetic restrictions. Takhtajan(1954) described that the evolution of plants is reflected in their ontogeny, and that ontogeny not

only reflects phylogeny but also forms the basis for their further evolution. According to this recapitulation theory, comparisons of ontogenetic changes among the related species may do much toward a better evolutionary understanding of ecology of the species.

In this paper distribution and habitat, and reproductive capacity and leaf development of Japanese species of Hosta are determined and their relationships are compared among the species from the viewpoint of ecology and evolution. Classification of Japanese Hosta is based on that of Fujita(1976a).

Distribution and Habitat

It is necessary at the first step for the study on life of species to clarify environments in which species lead an actual life. Distribution and habitat analyses with due regard to abundance are important in this sense.

The following is a list referring to distribution, habitat and abundance of Japanese species of Hosta. Distribution maps and habitat analysis were shown in previous papers(Fujita, 1976a, b).

Sect. Helipteroides F, Maekawa

H. sieboldiana (Lodd.) Engler. This species is common and distributed widely in southwest Hokkaido, Honshu, central Shikoku, and kyushu. It has such various habitats as valleys, grasslands, canopy openings and forest margins, growing both on rocks and on soils.

H. kiyosumiensis F. Maekawa. The range of distribution is fairly wide, covering south Kanto, Tokai and central and south Kinki. This species may be treated correspondingly as H. sieboldiana in habitat range in spite of a little occurring in wet places.

H. kikutii F. Maekawa. This occurs in south Kinki, Shikoku and southeast Kyushu. It grows on rocks in valleys. It is not rare but

limited in habitat range.

H. pycnophylla F. Maekawa. This is found only on relatively dry rocky soil on mountain ridges in Isl. Oshima(Yamaguchi Pref.), Chugoku.

H. hypoleuca Murata. This is restricted on rocks along valleys in Mikawa, Chubu.

Sect. Picniphylla F. Maekawa

H. longipes (Franch. et Savat.) Matsumura. This ranges widely from Honshu to Shikoku and Kyushu. It is not rare and not limited in topography of habitat but strictry confined epiphytically on rocks and tree trunks.

Sect. Nipponosta F. Maekawa

H. albomarginata (Hook.) Ohwi. This spreads over Japan, growing commonly in varied habitats other than dry places.

H. longissima Honda ex F. Maekawa. This is distributed in west Honshu, Shikoku and Kyushu. It is not rare but confined rigidly to low moors.

Sect. Stoloniferae F. Maekawa

H. alismifolia F. Maekawa. This is rare and only found in marshy places in Mikawa, Chubu, and Kochi City, Shikoku.

Sect. Tardanthae F. Maekawa

H. pulchella N. Fujita. This species exists only on rocks on a high ridge of Mt. Sobo, Kyushu.

H. tardiva Nakai. This is rather common in Shikoku, though it is often cultivated. It occurs on rocky soils.

H. tsushimensis N. Fujita. The range of distribution extends throughout Isl. Tsushima, Kyushu. It is common there in varied habitats except on wet soils.

H. tibai F. Maekawa. This is found only in Nagasaki City, Kyushu and also restricted to outcrops and rocky soils.

Sect. Eubryocles F. Maekawa

H. shikokiana N. Fujita. This grows only on outcrops on mountain ridges in central and west Shikoku.

Sect. Lamellatae F. Maekawa

H. capitata (Koidz.) Nakai. This is rarely distributed in Chugoku, Shikoku and Kyushu. It is mainly limited to outcrops of limestone.

Fujita(1976b) classified Japanese species fo Hosta into three types on the basis of preferred soil moisture conditions, and found that there is a positive correlation between habitat range and abundance of species. Present life and history of a species may be reflected in the pattern of distribution, the extent of habitat and the degree of abundance of this species. In this view Japanese species of Hosta may be roughly grouped into the following four types: (1) those which are distributed widely and commonly, and found in varied habitats, (2) those which have rather wide distribution range but occur in limited habitats, (3) those which show fairly wide but rare distribution, and grow in restricted habitats, and (4) those which are limited in both distribution and habitat. H. sieboldiana, H. kiyosumiensis and H. albomarginata belong to the first type. H. tsushimensis can be included in this type because of wide habitat range and high abundance, though it has not wide distribution range. H. kikutii, H. longipes and H. longissima fall into the second type. The third type is composed of H. capitata and H. alismifolia. The other species are attached to the last type, with a little differences among them.

Reproductive Capacity

In Hosta which consist of herbaceous perennials, observed are both sexual and vegetative reproduction by seed and ramet production.

Seed.

As for relations between seed number and weight of plants, and

their environmental conditions, Salisbury(1942) showed that, generally, plants of closed or stable communities produce a few large seeds and those of open or pioneer communities have many small seeds. Baker (1972) concluded that seed weights are higher, on the average, for taxa whose seedlings are exposed to the risk of drought soon after establishment in herbaceous plants. In those cases they related heavier seeds to a larger provisions of food reserves for the seedlings, enabling it to establish its leaf or root system quickly. Stebbins (1967, 1971) inferred that the selection for increased seed number or for larger seeds plays an important role in the adaptive radiation of higher plants.

Seed number and weight of Hosta are shown in Table 1, and seed size after air drying is given in Fig. 1. Seeds were collected from native sites throughout the range of distribution and habitat in each species. After eliminating ill developed seeds, seed number was counted and seed weight was measured after one week's drying at 95 C. Seed number per scape varies widely in every species, and it is difficult to determine seed fecundity in species. However, the range and the mean value of seed number per scape in each species may reflect the degree of productiyity in this species, though roughly. Seed weight is alos more or less variable within a species, but yet species differences clearly lie.

As indicated in Table 1, H. sieboldiana and H. albomarginata produce not only plentiful but also heavy seeds, and nearly the same obtains with H. kiyosumiensis and H. tsushimensis. A few but heavy seeds are seen in H. longissima and H. capitata. H. alismifolia and H. tardiva bear no vital seeds. The other species all produce light seeds; and their seed number varies from small to somewhat large, but it is limited as a whole. Thus, the species which have wide habitat

range and high abundance show high fecundity, while those which occur in restricted habitats and exhibit less abundance show relatively low seed productivity. As for seed weight, the species which are confined to stony outcrops and rocky soils, except for H. capitata, produce light seeds, whereas those which grow in varied or wet habitats have heavy seeds. H. capitata bears especially heavy seeds, in spite of occurring on outcrops. In addition, seed characteristics vary with the locality within a species to some extent. To give typical instances, as shown in Fig. 1, habitat and geographical differences in seed size are exhibited by H. siebodiana and H. albomarginata, respectively. In H. sieboldiana plants which occur in rocky places often produce lighter seeds than those which grow on soils, which is parallel to the interspecific differences. In H. albomarginata, generally, seed weight increases with the ascent of altitude.

Effective reproduction by seeds involves germination and development to maturity of the next generation(Crosby, 1966). It is not too much to say that large output of seeds increases reproductive capacity by improving survival chance on the whole. On the other hand, relative to seed weight, it is known that the rate of seedling growth is proportional to seed weight and heavy seeds possess advantage in competition (Harper et al., 1970), but reported were some cases where seedling vigor was not merely in proportion to seed weight(Wilcox, 1954, 1955; Shibles & MacDonald, 1962; Schweizer & Ries, 1969). Therefore, it must be examined how seed weight contributes to seedling vigor. Seedling emergence and growth were tested and compared between heavy and light seeds.

Germination test in different depths of sowing, made in sandy loam soil whose water capacity was 46% on dry weight base, is shown in Table 2. It is almost no more than 1 cm depth that light seeds

can emerge. In contrast, heavy seeds show the successful emergence from even 3 cm depth pretty well. Heavy seeds with large food stores have an advantage in the ability for emergence by epicotyl elongation in hypogeal Hosta seedlings. The compaction of soil complicates the effect of depth on seedling emergence, as pointed out by Triplett & Tesar(1960), but yet it is sure, from this result, that heavy seeds are more favorable than light ones for seedling emergence from seeds buried deeply in the soil.

Growth experiment in a experimental field was done under full light condition. Seeds were planted at 5 mm depth in the soil in spring, and seeling growth was followed, as listed in Table 3. Table 3 tells that seedlings grown from heavy seeds show rapid initial growth, and what is better, high drought resistance compared with those grown from light seeds. The soil in the field became considerably dry in late July after the rainy season in the course fo the experiment. Consequently the seedlings grown from light seeds, namely, those of H. kikutii, H. hypoleuca and H. longipes, died in short time probably because of shallow rooting, as shown in Fig. 2. Among deep-rooted seedlings grown from heavy seeds, on the other hand, those of H. sieboldiana, H. kiyosumiensis and H. albomarginata did survive, if not all; and those of H. capitata ended in death, though later than the shallow-rooted ones, probably because of low physiological drought resistance.

In parallel with this field experiment, seedling growth was examined in sand culture in order to account for relations between moisture gradient in the soil and root systems of seedlings in relation to seed weights. In spring seeds were sown in pots at 5 mm depth in sand whose water capacity was 16% on dry weight base, and during germination and subsequent initial growth seedlings had been cultivated under the condition of sufficient water supply. After the first leaves had developed culture conditions in pots were

changed into one of the following two water tables: (1) high water table, maintaining water surface 15 cm below the sand surface; and (2) low water table, 30 cm below. The pots were made with vinyl cover not to be exposed to the rain. In autumn after shedding of leaves, seedlings were harvested and their biomass was determined. Seedling weights and survival rates are represented in Table 4. Table 4 shows that, in low water table, seedlings grown from light seeds exhibit remarkably retarded growth and little survival, while those grown from heavy seeds display better growth and survival. Even in those of H. capitata and H. albo-marginata which died or suvived little in the case of the field experiment, good growth and survival are seen, because in sand culture constant water supplu is kept at deeper depth even in low water table.

These two experiments in Hosta give cases where differences in the type of seedling root systems significantly affect the seeling establishment, as shown with other plants(Toumey, 1929; Holch, 1931; Satoo, 1956), and it is elucidated by the experiments that heavy seeds undoubtedly increase reproductive capacity as far as Hosta is concerned.

These results appear, at first view, to be contrary to the fact that the species which have light seeds are less susceptible to drought than those which bear heavy seeds on the basis of relative growth rate of seedlings(Fujita, 1976b). However, experimental conditions are different between them, and it is just when grown in the soil where upwardly decreasing moisture gradient is seen that light seeds have a disadvantage in survival on account of shallow rooting. They are more resistant to drought than heavy seeds when raised under the same moisture stress. In Hosta, as found by Baker(1972) in coastral plants, light seeds are produced by the species which inhabit restrictedly outcrops and rocky soils, where, regardless of seed weight, there is a chance for germination and establishment of seeds only when they

are luckily dispersed in rock cvevices and on moss covers. These species may increase seed fecundity instead of making seeds heavier without disadvantage in survival as far as they limitedly occur in such habitats. This may be confirmed by the fact that their seed number per capsule is generally large in comparison with the species which have heavy seeds. On the other hand, the species which grow in various or wet habitats bear heavy seeds favorable for the establishment on the soil. Exceptionally H. capitata produces particularly heavy seeds in spite of occurring on outcrops, for it must compensate for physiologically high susceptibility to drought. Particularly heavy seed production causes low fecundity, still it do this of necessity, not of choice.

Ramet

Vegetative reproduction of Hosta is given by producing new buds on rhizomes every year. As shown in Fig. 3 and Table 1, many Hosta species have short rhizomes, but some species bear creeping rhizomes and easily release new ramets. In the former vegetative reproduction may play a part only in settling continuously in the place once established, whereas in the latter it may serve to spread distribution range to some extent. It is understandable that rhizome elongation is seen in H. albomarginata and H. longissima which grow in wet places, and H. tardiva which displays infertility. However, H. alismifolia which show infertility as well as occur in wet places does not elongate its rhizome, which characterizes its limited distribution and low abundance.

In Hosta species adaptive relationships between reproductive characteristics and environmental conditions of the habitat. This bespeaks the ecological significance of the parental relation, which is one of the important intraspecific relationships.

Leaf Development

Leaf characters which show ontogenetic changes are few in Hosta, but leaf shape is a hot lead to study ontogenetic changes of Hosta leaves. The fact the the change in shape from leaf to leaf on a stem, or ontogenetic heterophylly, in plants are well known(Goebel, 1898, 1908; Büsgen & Münch, 1929; Ashby, 1948, 1949). However, in most cases, attention is revited to heterophylly from interest only in juvenility. Ther are few studies on leaf development from the viewpoint of recapituration of phylogeny(Takhtajan, 1954; Dostal, 1959). Attempting to explain ecology and evolution of Hosta from such viewpoint, followed was the shape of successive leaves of a plant grown under full light condition in each Hosta species, except for H. slismifolia and H. tardiva which produce no vital seeds.

Leaf series of Hosta, as shown Figs. 4–10, are generally classified into the following four types: (1) lanceolate leaf with attenuate base lasts from young to adult stages ; (2) lanceolate leaf with attenuate base continues for young stage, but it change into linear leaf with cuneate base in adult stage; (3) nearly lanceolate leaf with attenuate base holds for young stage, and followed by oblong to ovate leaf with rotundate to cordate base in adult stage and (4) oblong to ovate leaf with rotundate to cordate base lasts from young to adult stage. The first type consits of H. albomarginata, and the second type is composed of H. longissima. H. sieboldiana, H. kiyosumiensis and H. tsushimensis belong to the third type. The other species, namely, H. kikutii, H. pycnophylla, H. hypoleuca, H. longipes, H. pulchella, H. tibai, H. shikokiana and H. capitata, constitute the last type.

Judging from ontogenetic changes of leaf shape, lanceolate leaf with attenuate base is probably juvenile form of Hosta. However, it was called in question that only the first leaves had a tendency to

be rotundate at base in the species which had lanceolate leaves with attenuate base in young stage.

It was found that experiments which offer unfavorable conditions cause plants to persist in producing juvenile leaves or to rever to the formation of juvenile leaves after adult leaves have been produced (Goebel, 1898, 1908; Ashby, 1948, 1949; Dostal, 1959). In order to give a full elucidation to the juvenile leaf form of Hosta, such experiments were done on Hosta seedlings and adult plants.

For seedling experiments seeds were germinated and seedlings were raised under one of the following three unfavorable conditions: (1) deep shade, germinating seeds and growing seedlings under the condition of 3% in light intensity in a greenhouse where the air temperature ranged from 25 to 15°C; (2) low temperature, germinating seeds at 3°C in dark over one year till sprouting of the first leaves and growing them in the greenhouse during the development; and (3) poor nutrition, cutting away cotyledons from seedlings when their first leaves peeped through epicotyls and raising them in the greenhouse. Under these unfavorable conditions, as given in Figs. 11 and 12, the attenuate leaf base was seen at least in the species which had it from the second leaf on in young age under favorable sonditions. This suggests that the appearance of the rotundate leaf base in the first leaves of these species may be attributable to cotyledon-like development, for the first leaves which first develop from hypogeal Hosta seedlings with undeveloped cotyledons are particularly well supplied with nutrition in seeds under favorable conditions.

For adult experiments, adult leaves were detached from plants just after their full development in spring to give internally poor nutritive conditions to the plants, and the shape of redeveloped leaves was observed. All the tested plants, as represented in Fig. 13, newly

developed lanceolate leaves with attenuate base. In addition, the same shape was found, as shown in Fig. 13, in autumn leaves which developed after the flowering season. According to Dostal(1959), these leaf form is caused by inhibitory effcts which can uncover psat evolutionary stages.

Thus the lanceolate leaf with attenuate base may be safely regarded as the juvenile form in Hosta. On the basis of the recapitulation theory, the juvenile form in ontogeny implys the ancestral form in phylogeny. In contrast to the appearance of the adult form from the first leaf development, the retention of the juvenile leaf form at least for young stage may be considered neotenic. Comparisons of leaf series among Hosta species, especially among the closely allied species, reveal that H. sieboldiana and H. kiyosumiensis, and H. tsushimensis are neotenic in leaf development as against H. kikutii and H. tibai, respectively. H. albomarginata which retains the juvenile leaf form throughout its ontogenymay be regarded typically neotenic, while, in comparison with this species, H. longissima, its closely related species, does not seem to be neotenic in spite of the display of juvenile leaf form in very young stage. It is a noteworthy fact that neotenic development is shown by the species which grow commonly in varied habitats and live a prosperous life in Hosta. The retention of young stage in ontogenetic development is related wth advanced mode of life in Hosta, as emphasized by Tabata(1966) in birches.

Neotenic development in ontogeny of a species may suggest at once its neotenic deviation in phylogeny. In this connection, it also deserve attention, in addition to above-mentioned relationships between the closely allied species, that scale-like abortive leaves, which represent rejuvenation(Foster, 1929; Dostal, 1959) and arise as a result of neotenic deviation(Takhtajan, 1954), often appears in seedlings

from nothern districts of distribution range in H. albomarginata, as shown in Fig. 7, and that H. sieboldiana generally maintains the juvenile leaf form up to later stage in ontogeny than H. kiyosumiensis, as indicated in Fig. 4.

Discussion and Conclusions

Takhtajan(1954) stated that there are principally three forms of adaptive evolution. One type of them is progressive evolution distinguished by a rise in the general level of organization and vital functions; another, specialization involving the elaboration of particular rather than general adaptations; and another, regressive evolution, or simplification of organization. As seen in H. sieboldiana, H. kiyosumiensis, H. albomarginata and H. tsushimensis, the high adaptability to broader conditions of environments founded on physiological and morphological progress, such as flexible water relations and plentiful and heavy seed production, makes possible for their species to grow commonly in wide ranges of both habitat and distribution. On the other hand, the other species which are characterized by narrow adaptability, for example, rigid water relations and light seed production, are limited in habitat range, though they adapt suitably themself to a particular environment. The former can be looked on as unspecialized or generalized in life, while the latter may be regarded as specialized in life. Thus advanced mode of life in Hosta is closely related to the enlargement of habitat range, whereas good adaptation to a limited habitat is accompanied by specialized mode of life.

Advancement of life in Hosta is founded in not merely the habitat enlargement but the change of relationships with other plants. Whittaker(1972) considered evolution of species in two aspects, namely,

niche differentiation and habitat one. In the case of Hosta, the species which are specialized in life occur in rocky places or moors, where competition among plants seems to be little in spite of physically and chemically severe conditions of environments. In other words, they may inhabit, so to speak, gaps in plant competition. On the other hand, those which are unspecialized in life can grow in grasslands and forests, where the competition may be relatively serious. It was shown that the specialized species exhibited low relative growth rates characteristic of stress-tolerant plants, whereas the unspecialized species displayed the capacity for rapid growth involved by competitive strategies of plants(Fujita, 1976b). This difference in the relative growth rate is probably a reflex of the difference in competitive relatioship with other plants. Therefore, it may be safely said that the advance of prosperous life of Hosta is connected with the acquirement of new relationsip with other plants base on the enhancement of competitive capacity.

Takhtajan(1961) stressed that the significance of neoteny in evolution lies in the despecialization, freed from the burden of specialization borne by the ancestral adult stages, which increasss the possibility of evolution in new directions. In the case of Hosta, it is worth while noting that H. sieboldiana, H. kiyosumiensis, H. albomarginata and H. tsushimensis which thrive in varied habitats, are neotenic in leaf development, every species of them. It is not too much to say that neotenic deviation has undoubtedly conduced to despecialization or advancement in life of species on the basis of broad adaptability, which is interpreted as progress evolution in Hosta.

Fujita(1976b) emphasized that the comparative analysis among the systematically related species is effective in studying the life of species from the viewpoint of adaptation, for these species are related

morphologically and physiologically. In addition, when the present life of species is discussed in evolutionary aspects, this comparative analysis may deepen the understanding of life of species, because the evolution of species is subjected to the restriction of phylogeny

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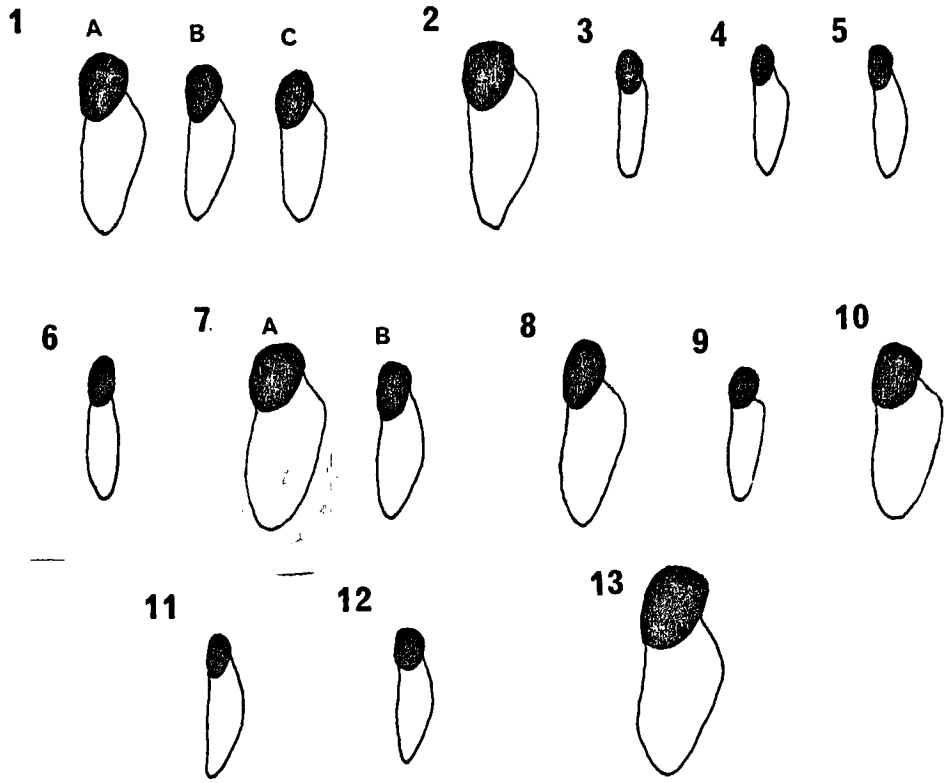

after air drying

Fig. 1. Seeds of Hosta on the scale of treble size. 1: H. sieboldiana, A: Mikata(Fukui Pref.), on moist soil in a stream bed, B: Togakushi(Nagano Pref.), on rock cliff, C: Hira(Shiga Pref.), on rocky soil on a ridge; 2: H. kiyosumiensis, Asama(Mie Pref.); 3: H. kikutii, Takakuma(Kagoshima Pref.); 4: H. pycnophylla, Oshima (Yamaguchi Pref.); 5: H. hypoleuca, Horai(Aichi Pref.); 6: H. longipes, Kitakomatsu(Shiga Pref.); 7: H. albomarginata, A: Ochiishi (Hokkaido), B: Ninnikusen(Nara Pref.); 8: H. longissima, Kakogawa (Hyogo Pref.); 9: H. pulchella, Sobo(Oita Pref.); 10: H. tsushimensis, Izuhara(Nagasaki Pref.); 11: H. tibai, Inasa(Nagasaki Pref.); 12: H. shikokiana, Ishizuchi(Ehime Pref.); 13: H. capitata, Niyodo (Kochi Pref.).

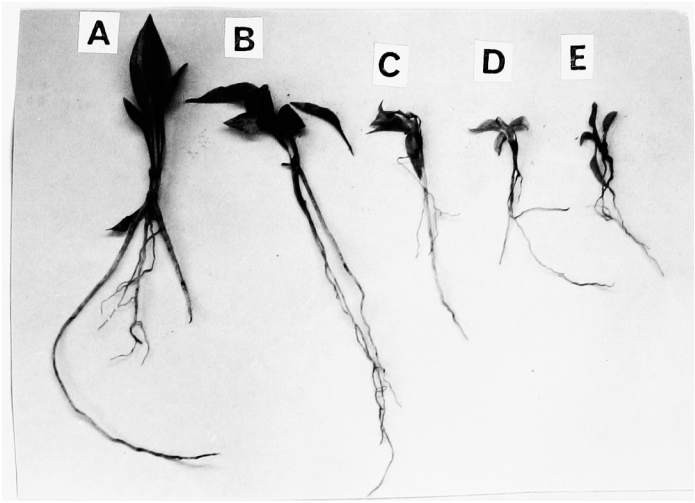

Fig. 2. Seedlings passing over the dry season in a experimental field under full light condition. A: a healthy deeper-rooted seedling of H. sieboldiana; B: a nearly dead deeper-rooted seedling of H. capitata; C, D and E: dead shallow-rooted seedlings of H. longipes, H. kikutii and H. hypoleuca, respectively.

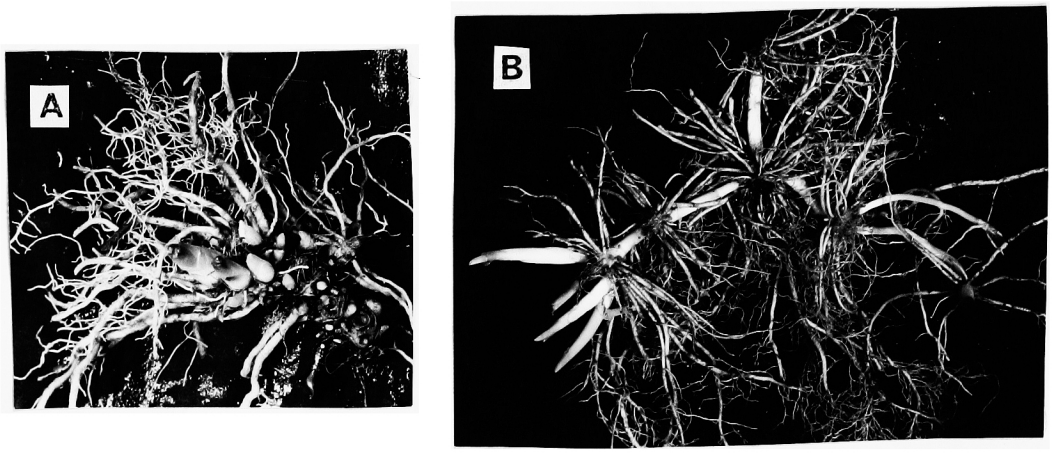

Fig. 3. Rhizomes of Hosta. A: short rhizome of H. sieboldiana, B: creeping rhizome of H. albomarginata.

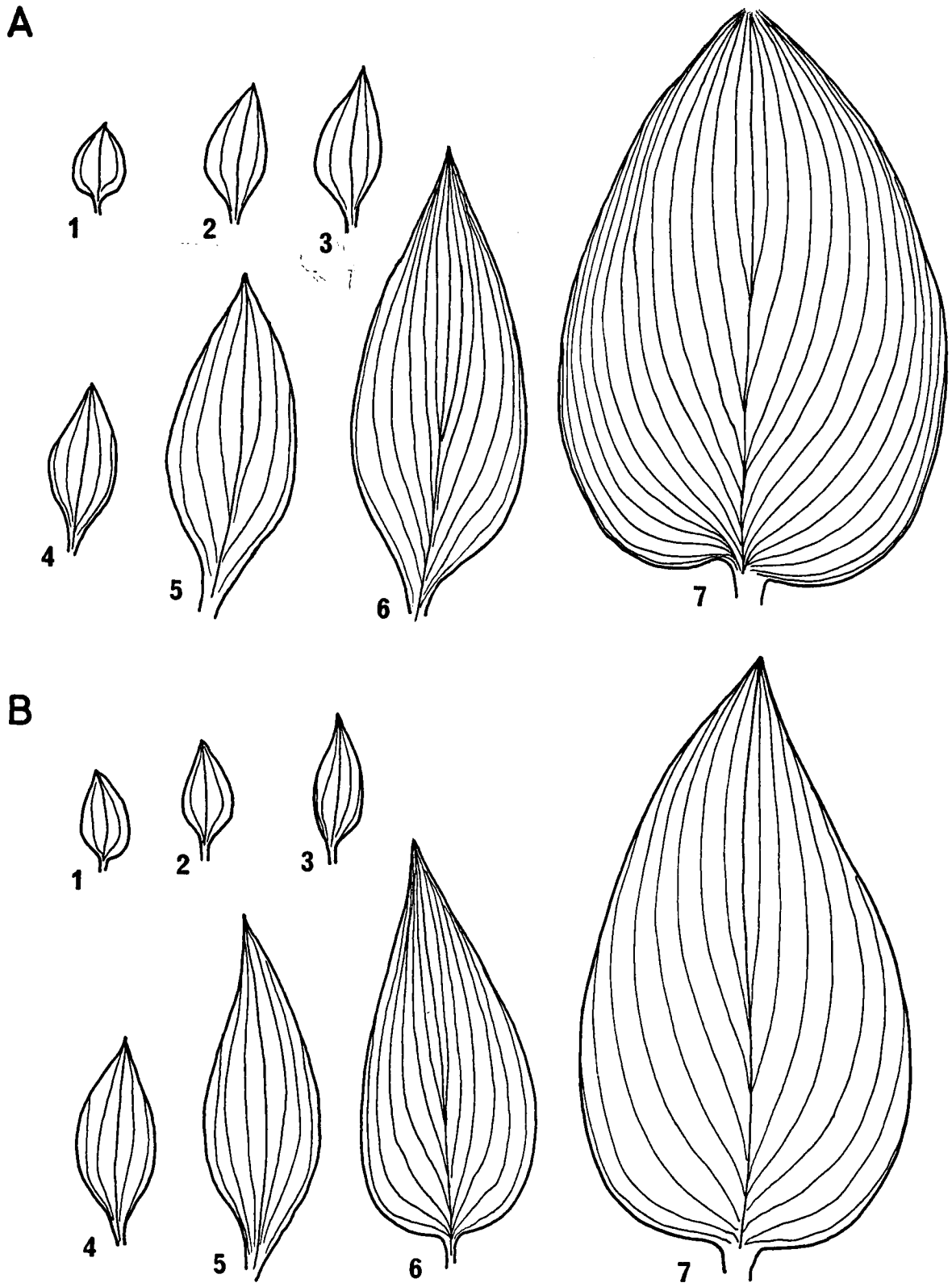

Fig. 4. Leaf series of Hosta. A: H. sieboldiana, Mikata(Fukui Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: juvenile leaf from four-year old plant on the scale of 1/2, 7: adult leaf on the scale of 1/4. B: H. kiyosumiensis, Takatsuki (Osaka Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf from four-year old plant on the scale of

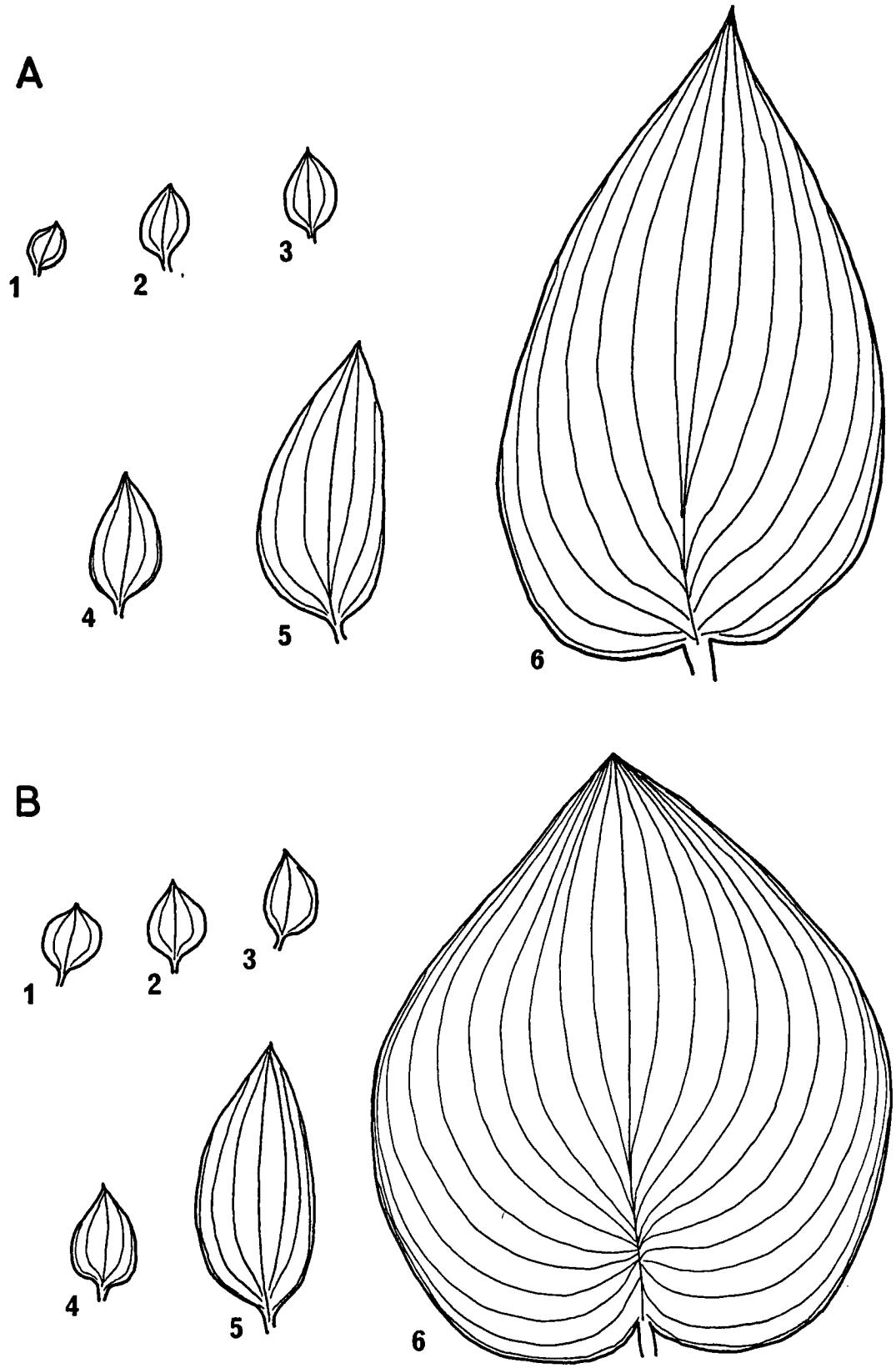

Fig. 5. Leaf series of Hosta. A: H. kikutii, Takakuma(Kagoshima Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf on the scale of 1/3. B: H. pycnophylla, Oshima (Yamaguchi Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf on the scale of 1/4.

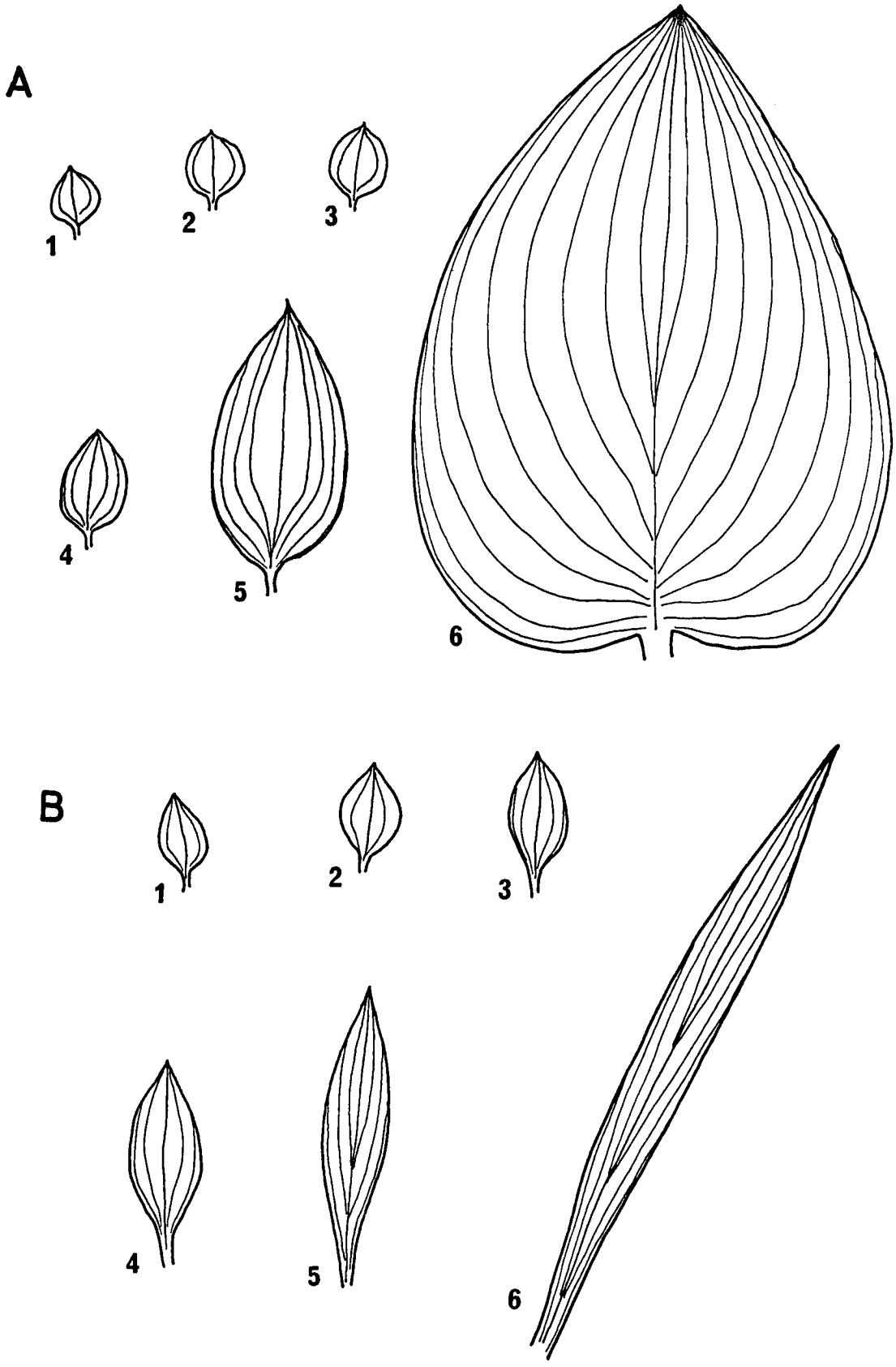

Fig. 6. Leaf series of Hosta. A: H. hypoleuca, Horai(Aichi Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: adult leaf on the scale of 1/4. B: H. longissima, Tsukude (Aichi Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf on the scale of 1/2.

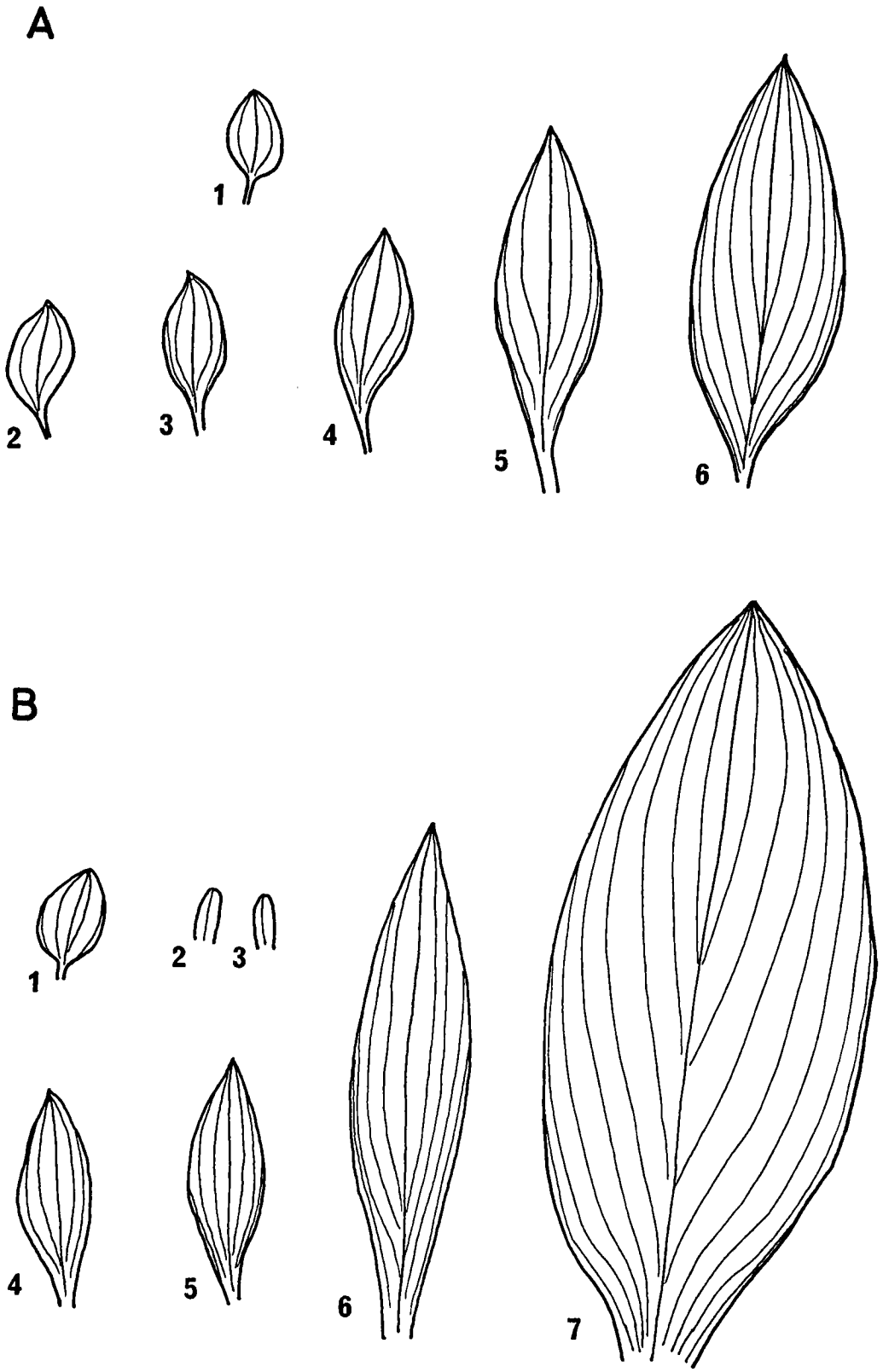

Fig. 7. Leaf series of Hosta. A: H. albomarginata, Unomachi (Ehime Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf on the scale of 1/2. B: H. albomarginata, Ochiishi(Hokkaido); 1: 1st leaf, 2: scale-like 2nd leaf, 3: scale-like 3rd leaf, 4: 4th leaf, 5: 5th leaf, 6: 8th leaf, 7: adult leaf on the scale of 1/3.

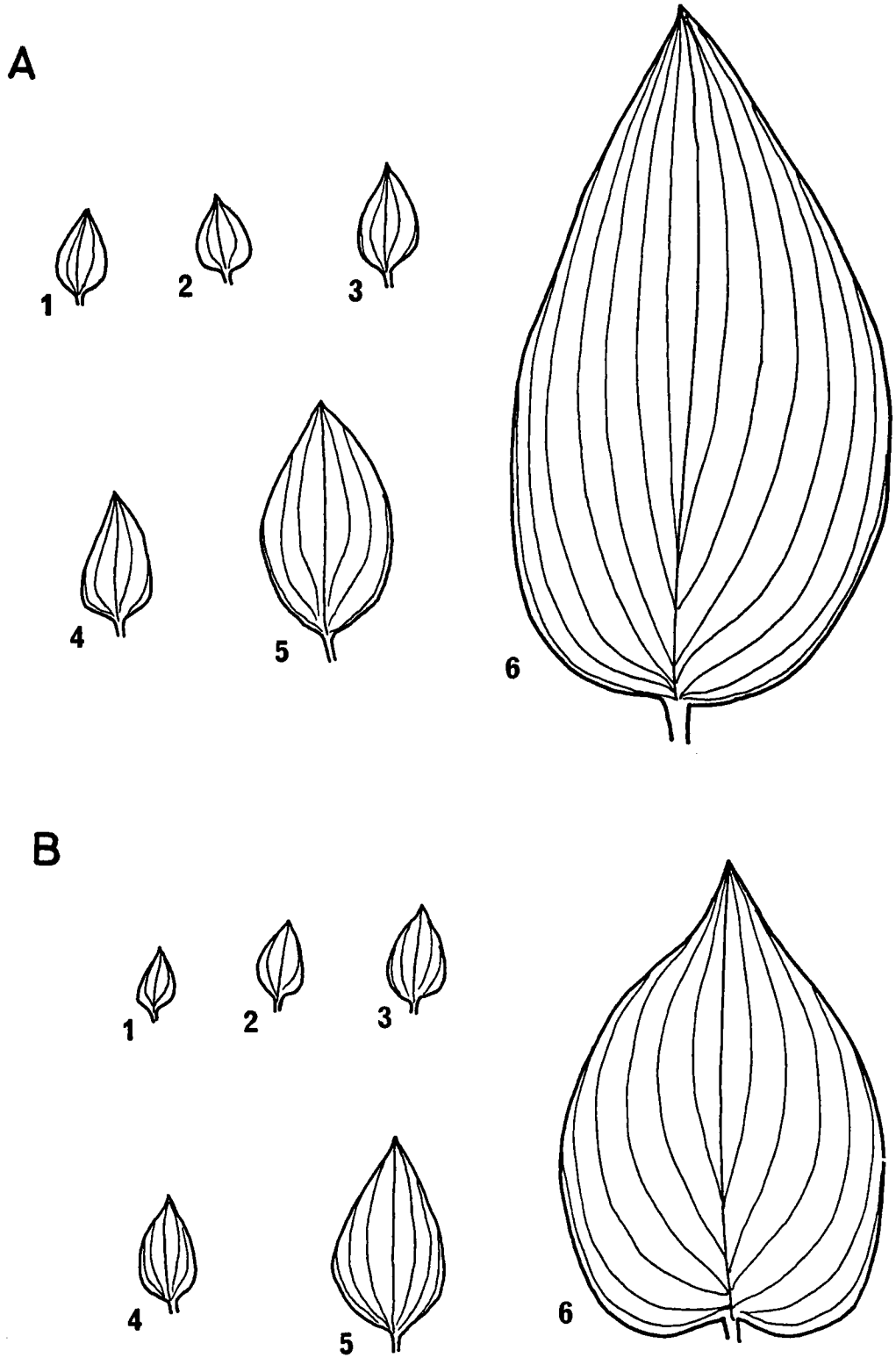

Fig. 8. Leaf series of Hosta. A: H. longipes, Kitakomatsu(Shiga Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: adult leaf on the scale of 1/3. B: H. pulchella, Sobo(Oita Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf on the scale of 1/2.

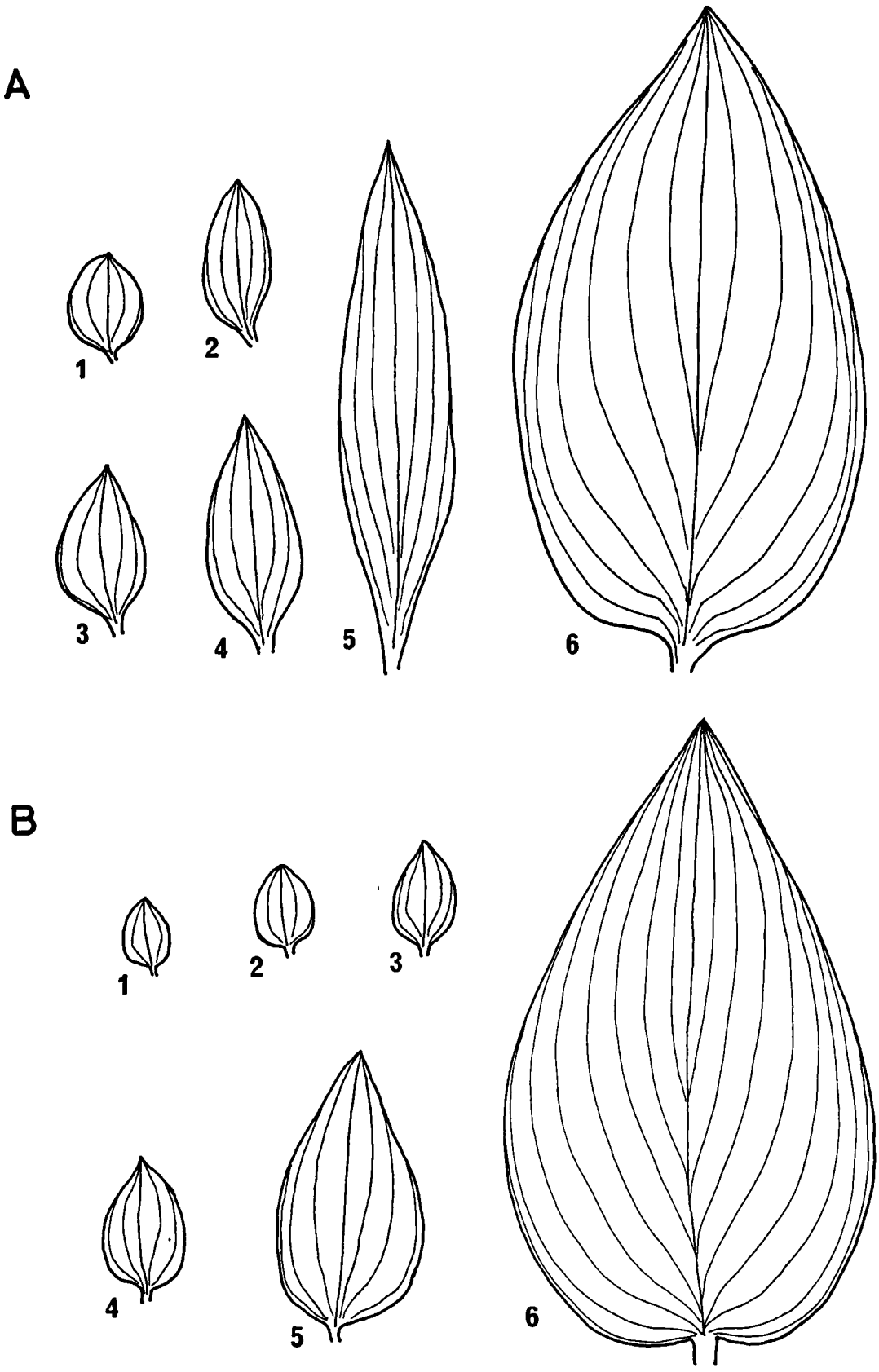

Fig. 9. Leaf series of Hosta. A: H. tsushimensis, Izuhara (Nagasaki Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf on the scale of 1/2. B: H. tibai, Inasa (Nagasaki Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: adult leaf on the scale of 1/3.

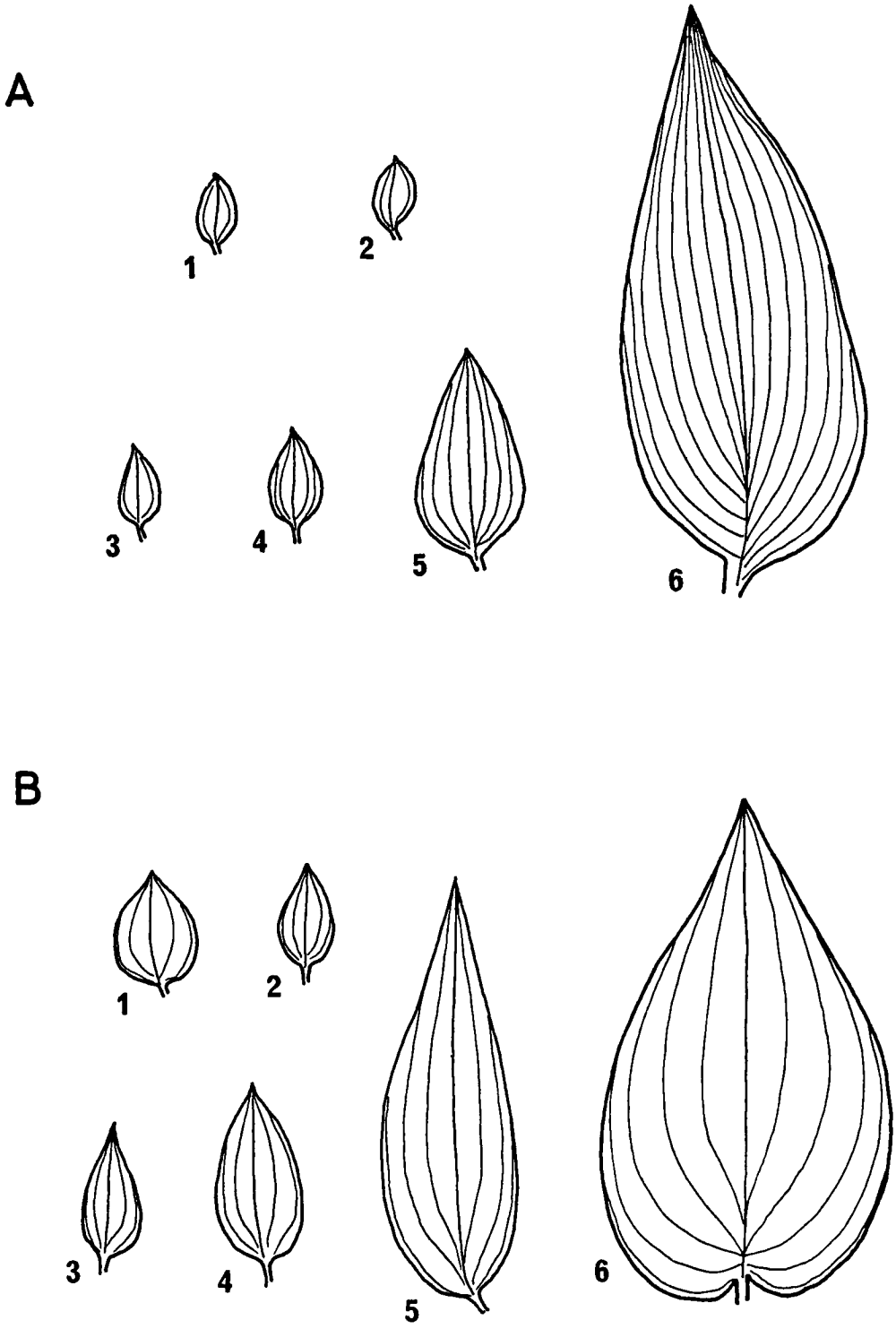

Fig. 10. Leaf series of Hosta. A: H. shikokiana, Ishizuchi (Ehime Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 7th leaf, 6: adult leaf on the scale of 1/2. B: H. capitata, Niyodo(Kochi Pref.); 1: 1st leaf, 2: 2nd leaf, 3: 3rd leaf, 4: 4th leaf, 5: 8th leaf, 6: adult leaf on the scale of 1/2.

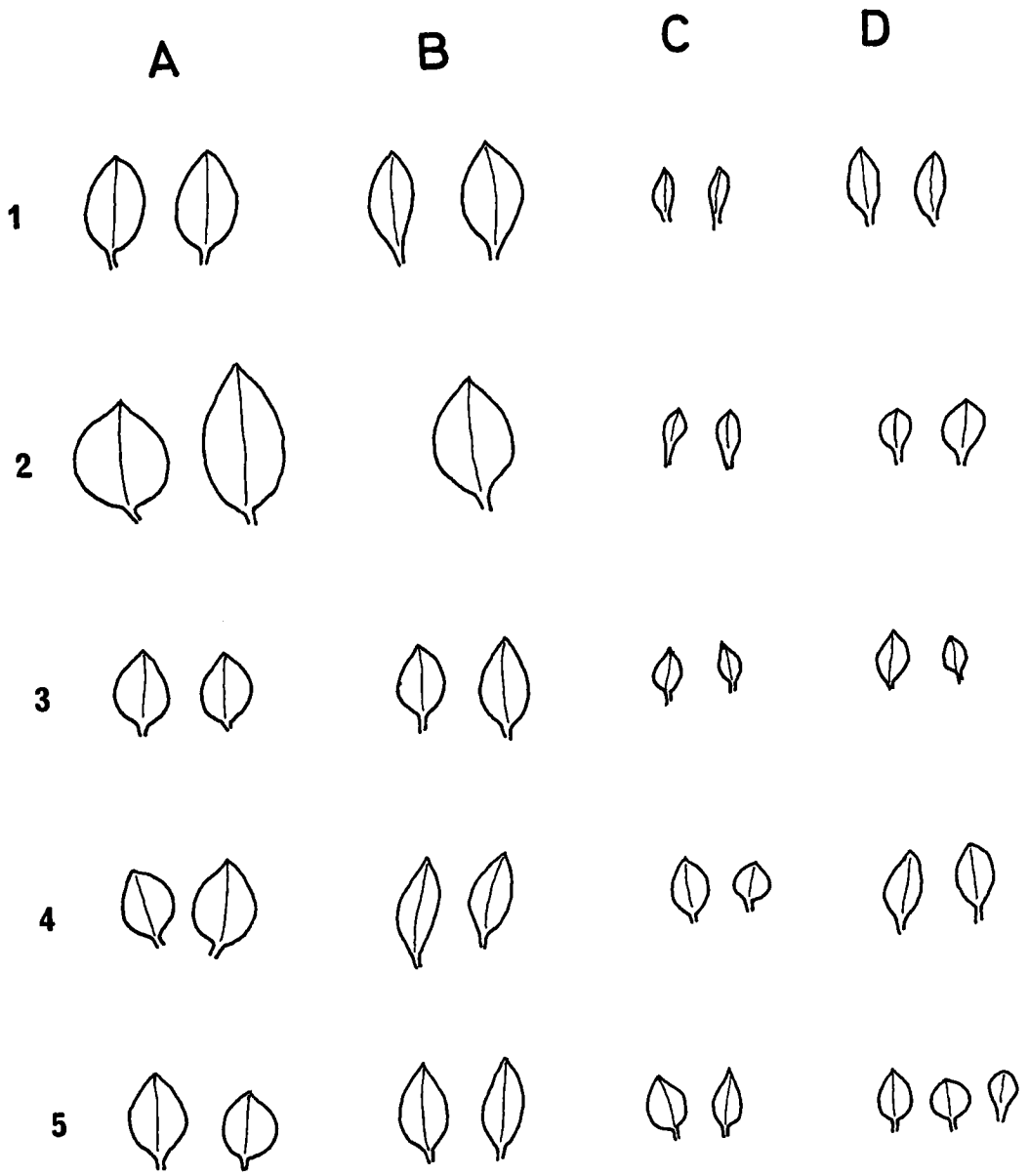

Fig. 11. The first leaves of Hosta under different growth conditions. A: favorable conditions, B: deep shade condition, C: low temperature condition, D: poor nutrition condition. 1: H. sieboldiana, Oeyama (Kyoto Pref.); 2: H. kiyosumiensis, Kashiwagi(Nara Pref.); 3: H. kikutii, Takakuma(Kagoshima Pref.); 4: H. hypoleuca, Horai(Aichi Pref.); 5: H. longipes, Fukuroda(Ibaragi Pref.).

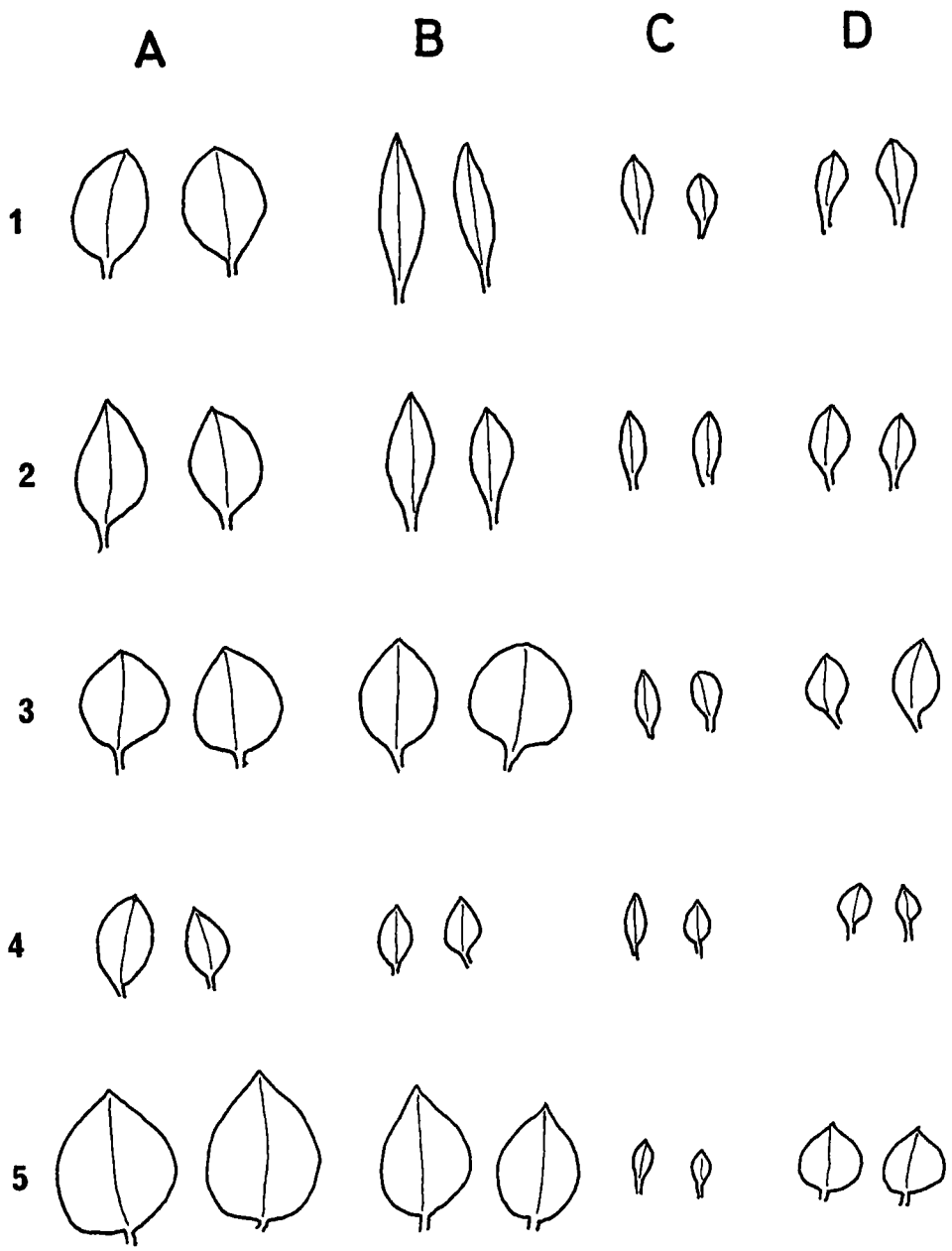

Fig. 11. The first leaves of Hosta under different growth conditions. Notes as Fig. 12. 1: H. albomarginata, Ochiishi(Hokkaido); 2: H. longissima, Kakogawa(Hyogo Pref.); 3: H. tsushimensis, Izuhara(Nagasaki Pref.); 4: H. shikokiana, Ishizuchi(Ehime Pref.); 5: H. capitata, Niyodo(Kochi Pref.).

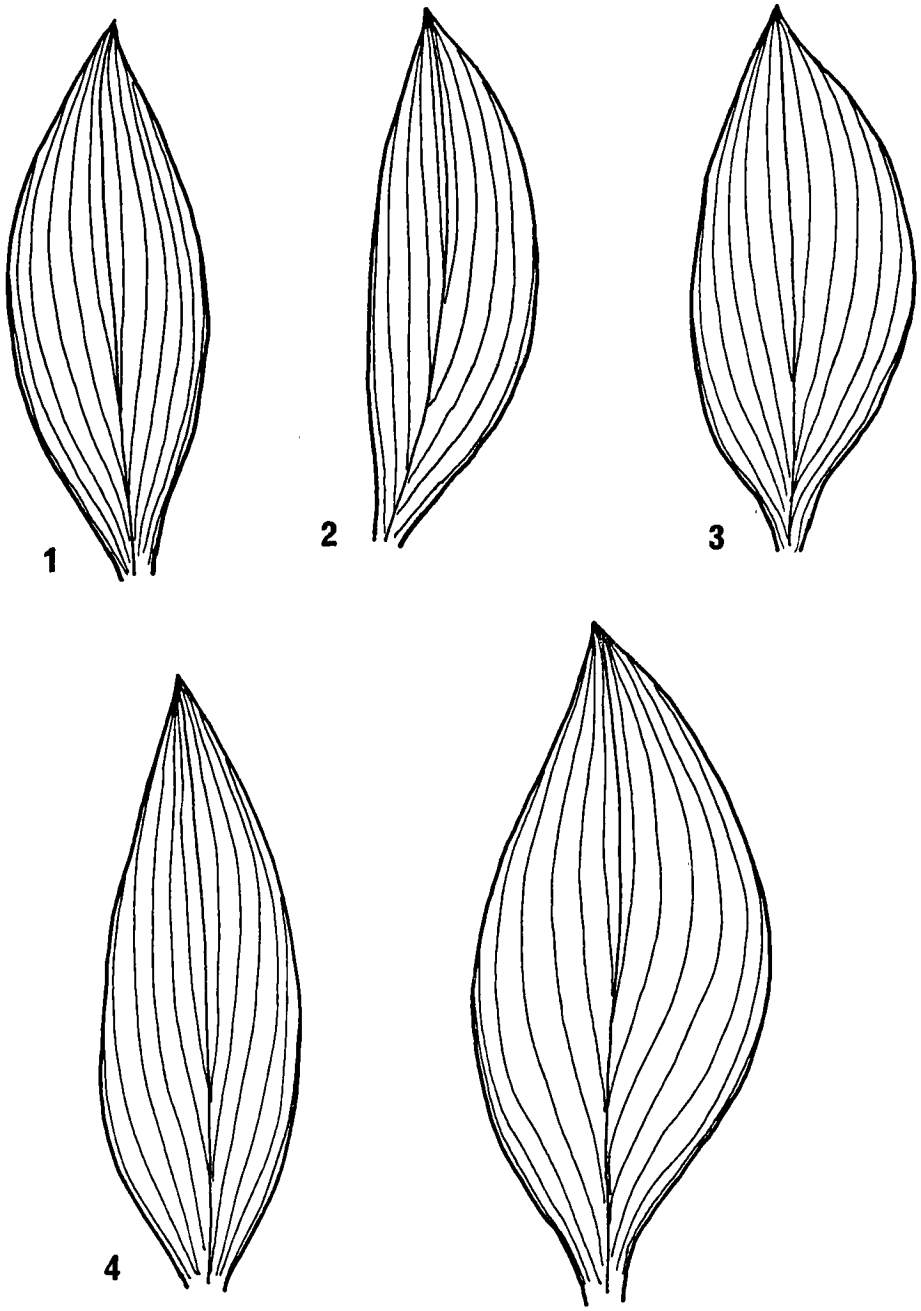

Fig. 13. Redeveloped leaves of adult Hosta plant. 1–4: after defoliation; 1: H. sieboldiana, Mikata(Fukui Pref.); 2: H. kikutii, Takakuma(Kagoshima Pref.); 3: H. pycnophylla, Oshima(Yamaguchi Pref.); 4: H. hypoleuca, Horai(Aichi Pref.). 5: autumn leaf after flowering season; H. sieboldiana, Noma(Kyoto Pref.).

Table 1. Reproductive charavteristics of Hosta. Each figure stands for the range of values with the mean value in a parenthesis. Presence of the ability to elongate rhizomes is presented by (+). Blanks indicate no ability in each characteristic.

Species	Seed number per capsule	Seed number per scape	Seed weight (mg DW per seed)	Rhizome elongation
H. sieboldiana	20–40 (29)	20–900 (250)	1.8–3.4 (2.9)	
H. kiyosumiensis	20–36 (27)	20–800 (180)	2.3–3.4 (2.8)	
H. kikutii	20–42 (33)	20–800 (130)	1.0–1.8 (1.3)	
H. pycnophylla	20–38 (31)	20–500 (120)	1.4–1.7 (1.5)	
H. hypoleuca	10–33 (19)	10–150 (40)	1.2–1.5 (1.3)	
H. longipes	20–42 (32)	20–500 (110)	1.2–2.0 (1.6)	
H. albomarginata	20–42 (26)	20–600 (200)	2.0–3.5 (3.0)	(+)
H. longissima	10–40 (21)	10–150 (60)	2.4–3.1 (2.8)	(+)
H. alismifolia				
H. pulchella	10–39 (28)	10–150 (50)	1.3–1.7 (1.5)	(+)
H. tardiva				(+)
H. tsushimensis	20–38 (24)	20–400 (180)	2.2–3.1 (2.7)	
H. tibai	20–40 (31)	20–150 (50)	1.3–1.6 (1.5)	
H. shikokiana	10–42 (32)	10–300 (90)	1.2–2.2 (1.8)	
H. capitata	10–30 (17)	10–200 (50)	3.3–4.7 (4.2)	

Table 2. Effects of seed weight on germination rate from different depth of sowing. Each figure of seed weight represents the mean value of 100 seeds, which is shown in mg DW, and that of germination rate stands for percentage. In each experiment 100 seeds were used.

Species and locality	Seed weight	Germination rate Sowing depth(cm) 0	1	2	3
H. sieboldiana					
Mikata(Fukui Pref.)	2.5	77	82	74	63
Oeyama(Kyoto Pref.)	2.6	87	86	67	76
H. kiyosumiensis					
Asama(Mie Pref.)	3.2	70	85	82	75
H. kikutii					
Tosayama(Kochi Pref.)	1.3	67	37	2	0
Yamakawa(Tokushima Pref.)	1.6	79	62	4	0
Takakuma(Kagoshima Pref.)	1.2	83	32	0	0
H. pycnophylla					
Oshima(Yamaguchi Pref.)	1.5	87	21	0	0
H. hypoleuca					
Horai(Aichi Pref.)	1.3	78	12	0	0
H. longipes					
Kitakomatsu(Shiga Pref.)	1.7	78	45	3	0
H. albomarginata					
Ochiishi(Hokkaido)	3.2	82	93	73	68
Ninnikusen(Nara Pref.)	2.5	77	83	64	52
H. longissima					
Kakogawa(Hyogo Pref.)	2.9	64	91	75	57
H. tsushimensis					
Izuhara(Nagasaki Pref.)	2.6	87	74	70	53
H. tibai					
Inasa(Nagasaki Pref.)	1.5	87	50	0	0
H. capitata					
Niyodo(Kochi Pref.)	4.2	76	90	63	68

Table 3. Seedling growth in a experimental field under full light condition. Each figure represents the mean value of 100 seeds or 20 seedlings. survival rates after the dry season are given in parentheses as the percentages of survival seedlings to germinated ones. Days after germination are indicated by 20, 50 and 80. L, R and T stand for leaf, rhizome and total seedling, respectively. Biomass is shown in mg DW.

Species and locality	Seed weight		Seedling weight 20	50	80	Survival rate
H. sieboldiana		L	2.0	19.0	43.5	
Oeyama		R	1.9	15.4	35.7	
(Kyoto Pref.)	2.6	T	3.9	34.4	79.2	(30)
H. kiyosumiensis		L	2.4	17.3	34.8	
Asama		R	2.0	13.5	28.4	
(Mie Pref.)	3.2	T	4.4	30.8	63.2	(20)
H. kikutii		L	0.7	4.0		
Takakuma		R	0.5	1.9		
(Kagoshima Pref.)	1.2	T	1.2	5.9		(0)
H. hypoleuca		L	1.0	4.9		
Horai		R	0.8	3.0		
(Aichi Pref.)	1.3	T	1.8	7.9		(0)
H. longipes		L	1.2	4.7		
Kitakomatsu		R	0.8	3.0		
(Shiga Pref.)	1.7	T	1.8	7.9		(0)
H. albomarginata		L	3.4	25.1	45.7	
Daihizan		R	3.3	18.0	51.2	
(Kyoto Pref.)	2.8	T	6.7	43.1	96.9	(5)
H. capitata		L	3.8	20.3		
Niyodo		R	2.7	16.2		
(Kochi Pref.)	4.2	T	6.5	36.5		(0)

Table 4. Seedling growth under low and high water tables in sand culture. Seedling biomass was measured in the first autumn. Each figure of biomass shows the average value of 100 seeds or all survived seedlings. Biomass is expressed in mg DW. Growth and survival ratios are given as the percentages of low water table to high water table.

Species and locality	Seed weight	Seedling weight Water table High	Low	Growth ratio	Survival ratio
H. sieboldiana Oeyama (Kyoto Pref.)	2.6	112.0	53.7	48	80
H. kiyosumiensis Asama (Mie Pref.)	3.2	135.0	118.0	87	67
H. kikutii Takakuma (Kagoshima Pref.)	1.2	66.7	4.0	6	6
H. pycnophylla Oshima (Yamaguchi Pref.)	1.5	64.2	6.7	10	2
H. hypoleuca Horai (Aichi Pref.)	1.4	37.7	5.7	15	4
H. longipes Kitakomatsu (Shiga Pref.)	1.7	92.0	15.1	16	16
H. albomarginata Ninnikusen (Nara Pref.)	2.7	105.2	36.1	34	60
H. longissima Kakogawa (Hyogo Pref.)	2.9	140.6	26.2	19	40
H. capitata Niyodo (Kochi Pref.)	4.2	167.0	119.7	72	40